University of Alberta

DENTITIONS OF THE EUGNATHOSTOMATA FROM THE LOCHKOVIAN (EARLY DEVONIAN) OF THE MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES, CANADA

by ©

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ABSTRACT

There are two hypotheses for the origin and evolution of teeth. The first is that they evolved from denticles lining the oro-pharyngeal cavity of early vertebrates; the second is that they evolved from scales that migrated into the oral region and became specialized.

The dentitions of fossil Eugnathostomata from the early Devonian MOTH locality in northwestern Canada, including eight putative chondrichthyans and six acanthodians, are diverse. The morphology, histology and distribution of teeth and tooth-like structures differ greatly within and among taxa.

Evidence from this study supports both hypotheses for the origin of teeth. Tooth-like labial scales of *Obtusacanthus* and *Ischnacanthus* are very similar to tooth whorls and teeth, while oro-pharyngeal denticles and plates of putative chondrichthyans resemble the tooth whorls in the same species. These examples can be taken to support both hypotheses, helping to frame the debate and suggest future research directions.

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LIST OF ABBREVIATIONS

Institutional and Locality Abbreviations

MOTH, Man On The Hill locality
NMC, National Museum of Canada, Ottawa
UALVP, University of Alberta Laboratory for Vertebrate Paleontology

Anatomical Abbreviations

aa, area of attachment
art, point of articulation
az, attachment zone
b, base of tooth
bt, basibranchial teeth
d, denticulation
dc, denticulated cusp
flp, finger-like projection
fp, fusion point
fs, fan-shaped scales
hs, head scale
k, keel
l, left
lbp, lower bony plate
lrtr, lower right tooth row
ls, labial scale
ltr, lateral tooth row
mc, mandibular canal
mk, Meckel's cartilage
mp, mosaic plate
ms, muscle scar
mtr, medial tooth row
pbc, piggy-back cusp
pc, pulp cavity
pce, primary cutting edge
pd, pharyngo-denticle
pq, palatoquadrate cartilage
psp, pointed stellate plate
r, right
rp, rosette plate
rs, rostral scale
sb, stellate branch
sc, stomach contents

sce, secondary cutting edge
sp, stellate plate
str, striation
stw, symphyseal tooth whorl
sym, symphysis
tc, tooth crown
tw, tooth whorl
ubp, upper bony plate
ultr, upper left tooth row
urtr, upper right tooth row
vc, vascularized canal
yc, youngest tooth crown

I. GENERAL INTRODUCTION

By the Early Devonian, gnathostomes were already well established and diversified into all of the major taxa both extinct and still living today (placoderms [Carroll, 1988], chondrichthyans [Miller et al., 2003], acanthodians [Waston, 1937], actinopterygians [Arratia and Cloutier, 1996], and sarcopterygians [Zhu and Schultze, 1997; Andrews et al., 2006]). Each of these groups also has a wide assortment of functional dentitions which include: dermal denticles, specialized labial scales, dentigerous bony jaws, tooth whorls, branchial/pharyngeal denticles, and palatine teeth. The different dentitions found in the gnathostomes from the MOTH locality are compared morphologically and structurally in hopes of finding some homologies and providing some resolution to the debate about the origins of teeth.

Definition of a Tooth

The development of teeth is important for understanding the origin and evolution of teeth. The most widely accepted hypothesis of tooth formation was developed by Reif (1982), who proposed the Odontode Regulation Theory. This theory was modified from the earlier Lepidomorial Theory (Stensiö, 1961) and Ørvig's odontode concept (1977).

Reif differentiated a tooth from a denticle, and his definitions are still well respected and accepted. He classified a tooth as an element of dentition formed from an odontode in a dental lamina, which prefabricates replacement teeth before the current tooth is shed (depending on the type of dental replacement pattern). A denticle, in contrast, is formed superficially at the epithelium-mesenchyme surface and does not originate in an invagination (not socketed). Teeth are also organized into families and rows, whereas denticles are typically less organized and do not necessarily have a pattern.

In his paper, Reif goes into the detail and classification of the different types of 'dentitions', from tuberculated dermal bones in heterostracans, to tooth plates in the Dipnoi within the gnathostomes and other various non-gnathostome other taxa (Thelodonti, Osteostracti, Galeaspida, Anaspida). For this study, I will focus on the dentitions of the gnathostomes, in particular the dentitions of presumed crown gnathostomes (i.e., the Eugnathostomata, see below).

The Odontode-Regulation Theory is a model currently used by researchers on both sides of the debate on the evolutionary origins of teeth (e.g., Johanson and Smith, 2003, 2005; Wilson and Hanke, 2003). I will use Reif's definitions for a tooth versus a denticle as a starting definition, but it may be changed or modified, based on the observations made in this study, as well as what is available in the published literature.

Evolutionary Origins of Teeth

There is a great deal of debate as to what constitutes a tooth, even with the definitions stated by Reif (1982). Is the definition based on morphology and structure, or is it based more on function? Smith and Johanson (2003) believed, for example, that some placoderms had evolved teeth, which they believed are functionally and structurally similar and homologous at some level to teeth seen in other jawed vertebrates.

Wilson and Hanke have noted some discrepancies in potential homologies between the teeth of early osteichthyans (bony fishes) and chondrichthyans (cartilaginous fishes) (Wilson and Hanke, 2003). They have presented evidence suggesting that the common ancestors of these two groups may not have had teeth and that each would have developed teeth independently. Wilson and Hanke have also pointed out that tubercles in some acanthodians were misinterpreted as teeth (Hanke et al., 2003).

The origins of teeth can be broken down by posing a few questions. What group was the first to evolve teeth? When in the fossil record did these teeth appear? Have teeth evolved more than once? Where in the body did teeth first appear (inside the margins of the mouth and/or the jaw, on the gill arches, etc)? These are all questions that are currently being debated.

There are two main hypothesized evolutionary origins for teeth. The first hypothesis is that teeth evolved from scales in the oro-pharyngeal region in early, jawless vertebrates (Johanson and Smith, 2003, 2005). Examples given for this type of evolution are the tooth-like, or tooth-whorl like pharyngeal denticulated plates seen in thelodonts such as *Loganellai scotia* (Smith and Coates, 2000).

The second hypothesis is that teeth originated from scales that migrated into the mouth and became secondarily specialized. This theory was first proposed by Hertwig (1874), who suggested that there were homologies between the placoid scales in sharks and the true teeth in higher vertebrates.

Unfortunately, even with these supported hypotheses, the evolutionary origins of teeth are still obscure. One line of evidence against the hypothesis for the origination of teeth from denticles in the oro-pharyngeal cavity of agnathans is that although there are tooth-like denticles in various thelodonts, these animals are not the sister group to the jawed vertebrates, which possess true teeth. Osteostracans are the generally accepted sister group to gnathostomes and they do not possess these tooth-like denticles (Donoghue and Sansom, 2002). It is also doubtful that placoderms had true, homologous teeth like those of the rest of the gnathostomes, though this is still an area of heavy debate (Young, 2003; Johanson and Smith, 2005).

The hypothesis suggested by Hertwig (1874), is directly contradicted by the hypothesis of the oro-pharyngeal origination of teeth. If placoderms and/or thelodonts possess true teeth, the condition seen in sharks must be derived, and not representative of the primitive condition.

The incompleteness and general lack of preservation of soft parts (i.e., the dental lamina) in the fossil record prevents direct observation of its presence. The majority of the gnathostome clades were well established and known from articulated specimens by the Devonian period. Unfortunately, most of these forms are only known from isolated scales previous to this time (Watson, 1937; Karatajute-Talimaa, 1992). This makes it difficult to assign a time and place for the origin of jawed vertebrates, as well as for tracing the origin and developmental modification of teeth throughout the vertebrates (Lison, 1954).

'Dentitions' in Gnathostomes

To be able to understand the dentitions seen in this study, a general overview of the various types of dentitions of gnathostomes present in the Early Devonian is required. These dentitions range from the tuberculated gnathals of placoderms to the complex dental plates of lungfish.

Placoderms are generally considered to be the most primitive jawed vertebrates (Donoghue and Sansom, 2002). They have jaws made up of large gnathal plates, the upper jaws consisting of 2 pairs of superognathals (anterior and posterior), and the lower jaw of a pair of inferognathals. These plates have large, shearing surfaces that occlude against one another, but they are not teeth, just modifications of the dermal armour most likely to aid in feeding (Janvier, 1996). It has been proposed that in the more derived forms of some of the arthrodire placoderms there is evidence for an organized pattern of dentition (Young, 2003; Johanson and Smith, 2005).

The Chondrichthyes possess cartilaginous jaws: the palatoquadrates are the upper and the Meckel's cartilages are the lower pair. Extinct and extant forms possess tooth families lining the upper and lower jaws margins (Williams, 2001).

In some extinct forms, chondrichthyans also possessed symphyseal or parasymphyseal tooth whorls (tooth families preserved on a solid, fused, recurved base; Hay, 1907, 1909). In addition to these teeth, many sharks have tooth-like pharyngeal denticles in the form of placoid scales (Nelson, 1970).

Within the Acanthodii, the jaws are also formed by the palatoquadrate and Meckel's cartilages. Associated with these cartilages, there are multiple types of dentitions (Fig. 1.1): tooth whorls (symphyseal, parasymphyseal, and lining the upper and lower jaw margins), dentigerous jaw bones, 'gill rakers,' and branchial and pharyngeal denticles. When teeth are present, there is usually more than one of these forms of dentitions present (Watson, 1937; Gross, 1971; Ørvig, 1973; Valiukevičius, 1992; Gagnier, 1996).

In actinopterygians, there is a change in the structure of the jaws. The palatoquadrate and Meckel's cartilages are very reduced and the primary tooth-bearing jaw elements are now the maxillary and premaxillary bones in the upper jaw and the dentosplenial bone in the lower jaw (Carroll, 1988). This condition is seen in the most basal actinopterygians *Dialipina* and *Cheirolepis canadensis*. In these fishes, there is a large assortment of different types of teeth and tooth-bearing elements in the mouth. There are multiple rows of replaceable teeth of varying sizes throughout the oral cavity (Arratia and Cloutier, 1996; Schultze and Cumbaa, 2001).

Sarcopterygians also have a diverse dentition, with multiple tooth-bearing bones in the jaws and inside the mouth, as well as tuberculations surrounding the

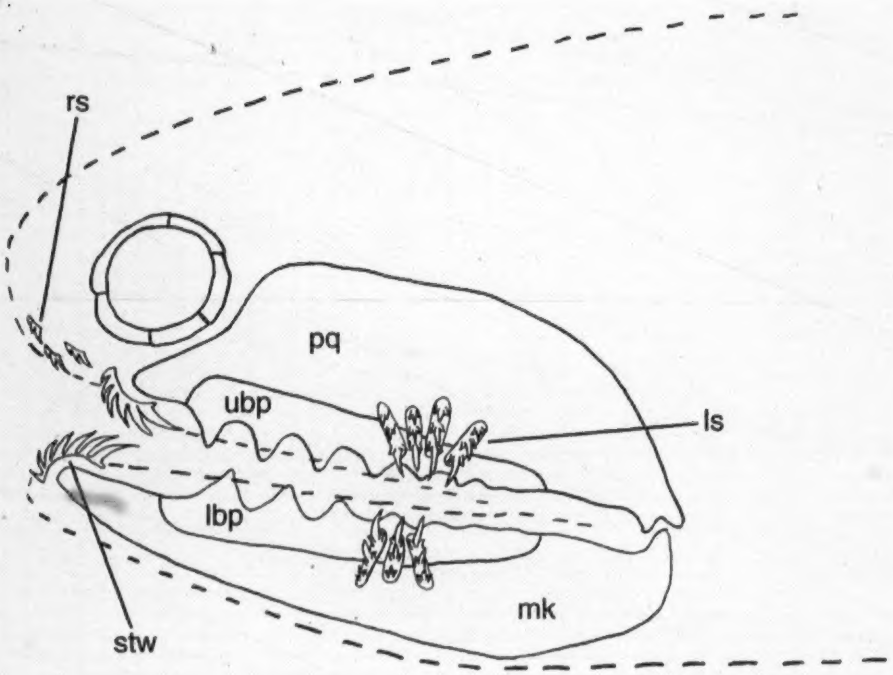

FIGURE 1.1. Acanthodian dentition showing the Meckel's and palatoquadrate cartilages, dentigerous overlying bony plates, symphyseal tooth whorls, and labial and rostral scales. **Abbreviations: lbp**, lower bony plate; **ls**, labial scales; **mk**, Meckel's cartilage; **pq**, palatoquadrate cartilage; **rs**, rostral scales; **stw**, symphyseal tooth whorls; **ubp**, upper bony plate.

socketed teeth (Zhu and Schultze, 1997; Andrews et al., 2006). Some of the early forms, such as *Onychodus jandemarrai*, possessed a parasymphyseal tusk whorl with replaceable teeth (Andrews et al., 2006).

As a final example, lungfishes have a very specialized and unique dentition. Many of the forms of lungfish possess tooth plates that are made up of initially isolated cusps that later fuse together. These plates are ankylosed to and become incorporated into the supporting jaw bones (Kemp, 2002).

The homologies and relationships among the varied dentitions discussed above are still unclear. It is doubtful that the denticles in the derived arthrodires are homologous to the lungfish tooth plates, but there may be some homologies between the various dentitions in the forms in between.

In this study I hope to add some detail to the known dentitions of the putative chondrichthyans and acanthodians. This information will hopefully be useful in better understanding how teeth and jaws evolved and changed, as well as how the primitive forms compare with the more derived ones.

Eugnathostomata

The term Eugnathostomata is often used to describe the crown group of gnathostomes (Chondrichthyes, Acanthodii, Actinopterygii, and other, higher vertebrates). Although this term has been used for some time, particularly on the internet, it was just recently defined in print by DeIuliis and Pulera (2007). They define the Eugnathostomata as separate from the Placodermi, because in the

Eugnathostomata, "the second visceral arch is modified into a hyomandibula, a supporting element for the jaw. In addition, eugnathostomes possess true teeth." This grouping of jawed vertebrates has been discussed before but has never formally been named or defined by distinct characteristics; they are often referred to as 'higher vertebrates' or 'crown gnathostomes' (Reif, 1982; Donoghue and Sansom 2002).

For this study, I will use the term Eugnathostomata when describing the taxa from the MOTH locality in northern Canada. The only representatives of this clade in the MOTH locality consist of putative chondrichthyans (as described by Hanke, 2001) and acanthodians.

Locality and Age

Vertebrate fossils from the MOTH (Man On The Hill) Locality, in the Mackenzie Mountains in the Northwest Territories of Canada, were first described by Dineley and Loeffler (1976) and by Bernacsek and Dineley (1977). The fossils and rocks collected from MOTH are part of the Delorme Formation and are of Lochkovian (Early Devonian) age. Fossils used in this study were collected by field parties of Dr. Brian D.E. Chatterton and subsequently by field parties of Dr. Mark V.H. Wilson over a number of years. The fossil-bearing rocks are interbedded light and dark calcareous siltstones and limestones. The sedimentologic and taphonomic conditions for this area have been represented as a topographic low (intra-shelf), below storm-wave base, often oxygen-poor, but occasionally oxygenated due to influxes of open marine water and storm events (Zorn et al., 2005).

The initial specimens studied by Bernacsek and Dineley, although well preserved, do not compare in quality to those found during later expeditions to the locality by the UALVP (University of Alberta Laboratory for Vertebrate Paleontology) and other associated institutions. Through careful preparation of the specimens, there have been some exquisite fossils found nearly completely preserved (e.g., the 'Wonder Block' described by Hanke and Wilson, 2006).

Goals of the Thesis

In this study, I will focus on the assorted dentitions of the early Eugnathostomata from this locality. I studied the morphology and structure of the teeth and tooth-like structures of eight putative chondrichthyans and six acanthodians.

I will be discussing the morphology, histology and distribution of the various dentitions in both the body of the different fishes as well as among the different taxa described. Emphasis is placed on jaw bones with and without teeth, tooth whorls and associated dentitions, and possible tooth precursors, with a comparison to other closely related species as well as other, higher forms within the Eugnathostomata. The results help to clarify the definition of teeth and related dental elements in these early fishes. They also add to the evidence concerning origins of teeth in jawed vertebrates, as well as possible modes of growth and development of the various structures.

Materials and Methods

The fossil fishes studied were recovered by using diluted acetic acid to etch away the matrix from fossiliferous slabs of rock. This was followed by gentle brushing with a very soft brush, and slow rinsing of the specimen in water. This process was repeated, as often as needed by the condition of the specimens, to remove the entire matrix. Isolated and smaller specimens were then placed on a piece of nylon mesh suspended in an ultrasonic bath filled with warm water and a small amount of mild detergent. All of the specimens were stabilized using 5% Glyptal™ cement dissolved in acetone.

Isolated whorls extracted from a single block, believed to be associated as remains of a single specimen, have been numbered individually. Each such associated specimen has been given the same specimen number, with the individual extracted whorls being identified by a decimal number following the specimen number (e.g., UALVP 42277.01, the first whorl extracted from specimen UALVP 42277).

Images of the specimens were taken using a Nikon Coolpix 4500 camera. High-magnification images were taken using the previously mentioned camera attached to a Nikon SMZ 1500 microscope. Certain specimens were whitened for photography using ammonium chloride sublimate.

Selected small specimens were imaged using a scanning electron microscope (SEM) for better morphological examination and description. These specimens were removed from the matrix and mounted on SEM stubs using water-soluble gum tragacanth. Larger specimens that were still embedded in matrix were attached to the stubs using double-sided tape for more support. The specimens were then sputter coated with a thin layer of gold before imaging to avoid polarization. Finally, the specimens were examined and digitally imaged in the SEM.

For histological study, specimens were analyzed using either a uct40 scanner (micro-CT scanner) or by thin-sectioning. The micro-CT scans were useful for larger resolution imaging of internal structures; this technique was used mostly for species for which there is only one specimen that could not be sacrificed for thin-sectioning. The data were further analyzed using computer programs Analyze and ImageJ v.1.37 to manipulate the files and data.

The thin-sectioning was done with imperfect specimens of species for which there were multiple specimens, in order to see more detailed histology of the internal structures of the teeth or whorls. These specimens were embedded in epoxy and then polished.

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II. OSSIFIED JAW BONES OF THE EUGNATHOSTOMATA FROM THE LOCHKOVIAN (EARLY DEVONIAN) OF THE MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA

INTRODUCTION

Evolution of Jaws

The vertebrates with jaws are collectively known as the Gnathostomata, and comprise the Placodermi (usually considered to be the most basal clade of jawed vertebrates), the Chondrichthyes, and the Teleostomi (Acanthodii plus Osteichthyes). In the strict sense, jaws consist of the cartilaginous palatoquadrate and Meckel's cartilages and their associated muscles, nerves, and bones (Nelson, 2006). It has usually been suggested that jaws originated by modification of the anterior-most gill arch in agnathans (Mallatt, 1996). It is also commonly accepted that osteostracans are the sister group to the jawed vertebrates (Donoghue and Sansom, 2002), and thus that they come closest to illustrating the jawless condition from which jaws evolved.

The origin and evolution of jaws is an interesting subject for which there are many unanswered questions (Smith and Coates, 2000; Donoghue and Sansom, 2002; Smith, 2003). How and when did jaws form? To what extent are jaws and associated, ossified jaw bones homologous across taxa? Are teeth a prerequisite for jaws/jaw bones or vice versa? These are just some of the largely unanswered questions involved in the search for a better understanding of jaw origins and evolution.

The most-basal known clade of gnathostomes is usually considered to be the Placodermi (Janvier, 1996). Placoderms possess unique dermal bones that form large parts of the functional jaw apparatus; however, there is no established homology of these bones to those in any other jawed vertebrates in the present or fossil record (Janvier, 1996). The homologies between the jaw structures of early fossil gnathostomes and corresponding jaws of extant relatives are most clearly seen in the chondrichthyans (Smith, 2003), for which the fossil representatives possess jaw structures very similar to those of their extant relatives. The situation with the strictly fossil Acanthodii and their extant relatives the Osteichthyes is also complicated, because acanthodians lack the associated, often tooth-bearing dermal bones and the endochondral bones that are characteristic of osteichthyans. As a result of these difficulties, there is no clear answer to the question of how jaws evolved and there are continuing debates about whether teeth evolved earlier than jaws or jaw bones, or vice versa (Smith and Coates, 2000).

Jaws in Devonian Vertebrates

By the Devonian period, jaws were already present in a wide variety of taxa, including Placodermi (Janvier, 1996), Chondrichthyes (Miller et al., 2003), Acanthodii (Hanke, 2001), Actinopterygii (Arratia and Cloutier, 1996), and

Sarcopterygii (Andrews et al., 2006). All of these taxa possess one or more types of associated dentitions, which are supported upon the jaws.

One of the issues with using the term 'jaw bones' in many different taxa is that it might be taken as indicating a homology between all of the structures so named, as well as indicating a possible homology to the jaw bones of higher vertebrates. For this study, 'jaw bones' is a functional term that defines the calcified or ossified structures of the mouth, usually supporting teeth, that aid in grabbing and biting food. There may also be a danger of relating the often-calcified jaw cartilages of Chondrichthyes to the dentigerous 'jaws bones' of acanthodians, and then, possibly, to relate the latter structures to the jaws of actinopterygians and other, osteichthyans. The differences between these structures must be clearly understood when describing the jaws of various taxa.

In the Placodermi, the functional jaws consist largely of large, armored gnathal plates. The upper jaw is usually made up of 2 pairs of superognathals (anterior and posterior) and the lower jaw of a single inferognathal. There is no evidence in placoderms for any structures homologous to the endochondral bones derived from the palatoquadrate and Meckel's cartilages of other vertebrates (Janvier, 1996).

In the Chondrichthyes, as well as in the putative chondrichthyans discussed in this thesis, the jaws consist of an upper pair of palatoquadrate cartilages and a lower pair of Meckel's cartilages (Carroll, 1988). Their specific morphologies may vary between species, but their overall structures are broadly similar. In most fossilized examples, these cartilages themselves are not preserved, and the only indication of their former presence is the teeth or tooth families found in place in the jaws (Williams, 2001). In some cases, these cartilages become calcified (Miller et al., 2003; Hanke, 2001), helping us to understand better their various morphologies, as well as their homologies with comparable elements in other taxa, including acanthodians.

In the Acanthodii, the jaws consist of a combination of palatoquadrate and Meckel's cartilages overlain, in some taxa by dermal, dentigerous bony plates. Within the Ischnacanthiformes, what are traditionally referred to as 'jaw bones' are simply the dentigerous bony plates. Unfortunately, in many cases the cartilages in these fish were not calcified or preserved, leaving only the bony 'jaws' preserved in the fossil (Bernascek and Dineley 1977). This type of preservation can lead to misinterpretation of acanthodian 'jaw bones' as somehow homologous with the often-calcified, cartilaginous jaws seen in the Chondrichthyes. Some researchers have emphasized that the jaws of these acanthodians consist of more than just these bony plates, but still insist on calling them jaws (Denison, 1976). Others simply ignore the differences and refer to the bony plates as the jaw bones, completely ignoring the associated cartilages and the implication of the inferred homologies (Ørvig, 1973).

In *Cheirolepis canadensis*, often considered the most primitive actinopterygian (Arratia and Cloutier, 1996), with the possible exception of *Dialipina* (Schultz and Cumbaa, 2001), the affinities of which are less certain, both the upper and lower jaws are made up of an assortment of bones. The upper jaws are composed of maxillary and premaxillary bones; the lower jaws consist primarily of the paired dentosplenials (Arratia and Cloutier, 1996). All three of these pairs of bones, as well as the other bones of the palate and medial side of the lower jaw, are tooth bearing in *Cheirolepis*.

In other early actinopterygians, such as the Palaeonisciformes, the tooth-bearing dermal jaw bones consist of maxillae and premaxillae in the upper jaw, and dentaries as the main tooth-beaing dermal bones in the lower jaw. The palatoquadrate and Meckel's cartilages are still present in the jaws but their extent is greatly reduced compared to the chondrichthyan or acanthodian condition, the jaws now consist mainly of endochondral bone, and they are closely associated with the articulation of the jaw (Carroll, 1988).

In early sarcopterygians, the jaws are composed of similar bones to those seen in actinopterygians. One of the significant differences between the two dentitions of these fishes is the pair of symphyseal tooth whorls found in the lower position in the sarcopterygians (Zhu and Schultze, 1997; Andrews et al., 2006). In some exceptionally well preserved specimens, the growth and replacement mechanisms of these whorls can be seen in the jaws (Andrews et al., 2006).

In fossil and modern lungfish the jaws are very specialized and derived. In these fish, the teeth become fused together and subsequently ankylosed to their supportive jaw bones (Kemp, 2002).

Eugnathostomata from the MOTH Locality

This chapter focuses on the jaws of Eugnathostomata (see Chapter I) known from MOTH. So as not to further confuse the structural and functional homologies, when using the term 'jaws', I am referring to the palatoquadrate and Meckel's cartilages. If the species being described have additional structures associated with the jaws, as seen in *Ischnacanthus* spp., I will further specify the structures and refer to the overlying bony plates as the 'dentigerous jaws'. These bony plates are generally tooth-bearing and concave in their base where they fit over their supporting cartilages. This terminology will, hopefully, reduce the confusion with respect to implied homologies.

Acanthodian, chondrichthyan, and putative chondrichthyan remains have been found in rocks dating as far back as the Late Silurian and questionably in the Ordovician (Karatajute-Talimaa, 1992), while articulated specimens have been found in rocks from the Early Devonian (Watson, 1937; Miller et al., 2003). These fossils provide some insight into how and when jaws developed as well as how they compare and differ between the three groups.

The putative chondrichthyans discussed in this chapter were considered to be doubtful of relationship to chondrichthyans until Hanke (2001) studied the various specimens from the MOTH locality. From these exquisite specimens, Hanke was able to establish morphological features (fin spines, scales) that separated these putative chondrichthyans from the remainder of the Chondrichthyes, but also other features that separate these forms from acanthodians and suggest that these species might represent very early branches off the main chondrichthyan lineage. The first description of the calcified jaws of one putative chondrichthyan, *Kathemacanthus rosulentus*, was in the thesis by Hanke (2001) and the published description is now in press (Hanke and Wilson, in press).

Chondrichthyan jaws, consisting of calcified palatoquadrate and Meckel's cartilages, usually supporting a battery of teeth, have been found throughout the fossil record of the group, including in the oldest articulated chondrichthyan, *Doliodus problematicus*, from the Lower Devonian of Canada (Miller et al., 2003). These jaws are not ossified dermal bones, but cartilage that has become calcified allowing it to be preserved in the fossil record. Chondrichthyan calcified cartilage is usually of a particular type, called 'globular' or 'prismatic' (Cappetta, 1987), and this characteristic is seen in some of the putative chondrichthyans from MOTH as well.

Articulated remains of jaws of acanthodians, consisting of palatoquadrate and Meckel's cartilages, sometimes with overlying dermal plates, have been found in rocks as old as the Early Devonian (Denison, 1976; Gross, 1971). These cartilages are usually secondarily ossified, while the overlying bony plates are dermal bone (see below).

It was initially thought that only two families of acanthodians possessed bony jaws, the Diplacanthidae and Ischnacanthidae, with only one of these families having dentigerous jaws, the Ischnacanthidae (Watson, 1937). Gross

(1971) added the Climatiidae to the group with dentigerous bones with the discovery of dentigerous jaws belonging to *Nostolepis striata*. These jaws, although strikingly similar to those of the Ischnacanthidae, were classified in *Nostolepis* based on the associated scale morphology. I agree with Denison (1979) and Hanke et al. (2001) that these jaws should most likely be assigned to a new genus within the Ischnacanthidae, and that dentigerous jaws are not found within the Climatiidae. From this study, it is clear that at least two families of acanthodians possessed dermal bones with or without teeth (Ischnacanthidae and Diplacanthidae).

Little work has been done to understand better the histology and growth of these different bony plates. Gross (1971) and Ørvig (1973) were among the first and last to try to understand better how these structures developed and grew. Gross proposed that the dentigerous bony plates were repeatedly shed and regrown throughout ontogeny. Ørvig suspected that these plates continually grew throughout the life of the fish, adding new larger teeth to the anterior portion of the bone. Limited research has been done since these publications in the form of morphological observations (Hermus, 2003; Valiukevičius, 1992), but without detailed histological work, few firm conclusions can be drawn.

This chapter is an overview of the different types of calcified and ossified jaws, with associated bony and dentigerous plates where present, within the Eugnathostomata from the MOTH locality. Jawed fishes from this locality were first described by Bernascek and Dineley (1977), who found several specimens of what they identified as *Ischnacanthus gracilis*, as well as some unknown dentigerous plates, most of them attributed to the Ischnacanthidae.

It was not until later expeditions by UALVP personnel that many more and better preserved specimens were found and expertly prepared, allowing a greater knowledge of the diversity of these jawed vertebrates. From this locality, there are now known at least 6 different species with preserved or partially preserved (calcified and/or ossified) jaws and dentigerous bony plates. This study will examine in greater detail the different morphologies that these jaws take within the various species. It is hoped that this will, in turn, help to clarify the evolution of jaws and teeth in early vertebrates.

Terminology and Methods

Some anatomical terminology must be clarified prior to beginning the morphological descriptions of the different jaws. Because many of the elements studied can be found isolated, it is not always clear if we are looking at the upper or lower dentigerous jaws/bony plates, especially in the case of the dentigerous jaws of the ischnacanthids.

The front of the jaws will be referred to as anterior, the back of the jaws, posterior (Fig. 2.1A). When referring to the ventral or dorsal part of the jaw, I am referring to the bottom or top (respectively) of the jaw or dentigerous plate, and not its relative position in the mouth (Fig. 2.1A). If there are multiple rows of teeth, the main (usually the largest) row is referred to as the lateral row, and the

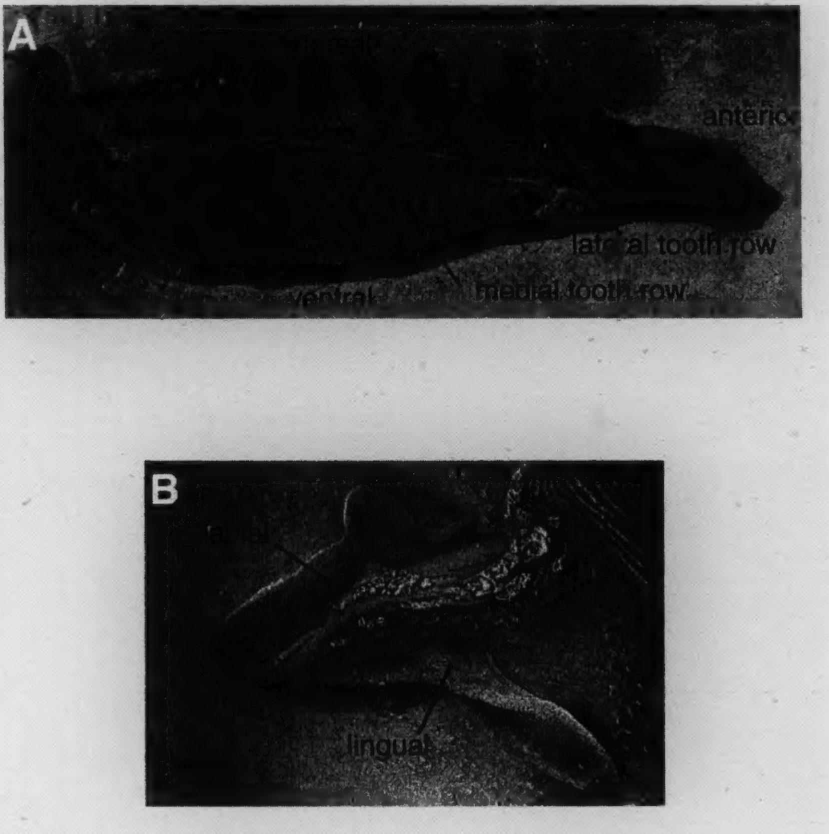

FIGURE 2.1. Clarification of anatomical terms. **A**, UALVP 45074, jaw of *Ischnacanthus* sp.(scale bar equals 1cm); **B**, UALVP 47074, *Gladiobranchus probaton* (scale bar equals 1mm).

smaller rows of teeth are referred to as the medial rows (Fig. 2.1A). When referring to a structure facing the inside of the mouth, I use the standard dental term lingual ('toward the tongue', even if there is no true tongue), and when a structure is facing toward the outside of the mouth, I will use the standard term labial ('toward the lips' even if there are no true lips) (Fig. 2.1B).

For complete methods, and locality and age information, see Chapter I.

Institutional and Locality Abbreviations—**MOTH**, Man On The Hill locality, Northwest Territories, Canada; **NMC**, National Museum of Canada, Ottawa; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton.

Anatomical Abbreviations—**art**, point of articulation; **d**, denticulation; **hs**, head scale; **l**, left; **lbp**, lower bony plate; **ls**, labial scale; **mk**, Meckel's cartilage; **ms**, muscle scar; **pc**, pulp cavity; **pq**, palatoquadrate cartilage; **r**, right; **rs**, rostral scale; **sym**, symphysis; **tw**, tooth whorl; **ubp**, upper bony plate.

SYSTEMATIC PALEONTOLOGY

Superclass GNATHOSTOMATA
EUGNATHOSOMATA DeIuliis and Pulera 2007
Class CHONDRICHTHYES Huxley, 1880
Order incertae sedis

Family KATHEMACANTHIDAE Gagnier and Wilson, 1996

Genus *KATHEMACANTHUS* Gagnier and Wilson, 1996

KATHEMACANTHUS ROSULENTUS Gagnier and Wilson, 1996

(Fig. 2.2)

Revised Diagnosis—Diagnosis based on oral region; for additional diagnosis, see Gagnier and Wilson (1996:243). Small putative chondrichthyan; palatoquadrate and Meckel's cartilages calcified with extremely long symphysis; possible globular calcified cartilage; lacking teeth, other dentigerous structures.

Holotype—UALVP 32402.

Referred Material—UALVP 43113, 47081.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—This revised description is limited to the 'jaws' of *Kathemacanthus rosulentus*; for a full description, see Hanke (2001:204-219), and Hanke and Wilson (in press). What appear to be upper and lower jaws of *K. rosulentus* are more precisely the calcified palatoquadrate and Meckel's cartilages (Fig. 2.2). The cartilage is most likely of the globular calcified type, judging by the grainy texture. Overlying the cartilages, there are no 'jaw bones' as seen in some of the acanthodians studied (see below). Unfortunately, the UALVP collection only has three specimens of *K. rosulentus*

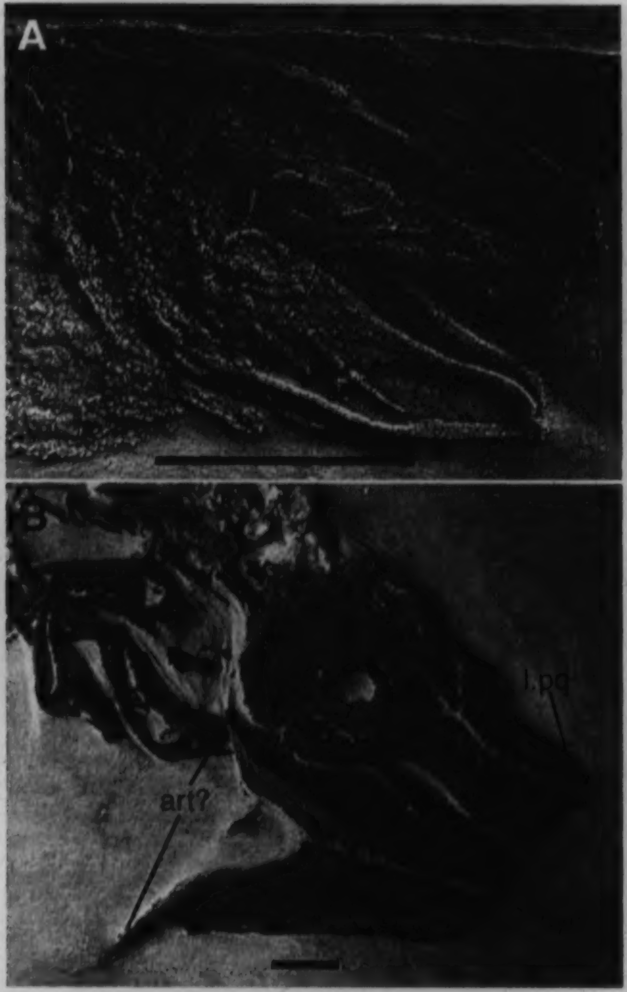

FIGURE 2.2. *Kathemacanthus rosulentus.* **A**, UALVP 43113, the most complete specimen of *K. rosulentus*, only the anterior portions of the cartilages are visible, the posterior portions are covered in scales; **B**, UALVP 47081, this specimen shows only the cartilages, note the key-shaped palatoquadrate and the long symphysis between the Meckel's cartilages. Scale bars equal 1cm.

with the calcified cartilages preserved, and the descriptions are mostly from UALVP 47081.

Palatoquadrate Cartilage—The palatoquadrate cartilages are calcified and large. The calcified part of the cartilage does not appear to be as thick as that seen in the Meckel's cartilages, but they are larger. The palatoquadrate is key-shaped and there is a circular hole in the posterior part of the cartilage (Fig 2.2B).

The anterior half of the palatoquadrate, making up the upper part of the rostrum, is long and smooth, with a rounded anterior end. Half-way back on the rostral part of the palatoquadrate, there is a thickened, calcified ridge that starts at the top of the cartilage and curves down to the bottom (Fig. 2.2B), where the posterior half of the palatoquadrate begins.

This posterior half of the palatoquadrate is thicker than the anterior half and is rounded. In the middle of this portion of the palatoquadrate, there is a circular hole, which is reinforced by a thickened ridge of calcification (Fig. 2.2B). It appears that this hole is part of the structure of the cartilage and is not an artifact of preservation. It may have been due to a healed injury or parasite that attacked the animal sometime during its earlier life.

The posterior portion of the palatoquadrate is only visible in UALVP 47081 (Fig. 2.2B), a specimen that only has preserved cartilages, and no scales. The outline of the key-shape can be seen in UALVP 43113, but no detail can be seen (Fig. 2.2A). Unfortunately because these are the two specimens with preserved mouths and jaws, little else is known about the posterior portion of the cartilage and whether the structures seen in UALVP 47081 are true for all specimens of *K. rosulentus*.

The symphysis between the left and right palatoquadrates extends to at least the anterior, rostral portion of the cartilage. There is no clear point of articulation between the palatoquadrate and Meckel's cartilages that is visible in either of these specimens (Fig. 2.2).

Meckel's Cartilage—The Meckel's cartilages, also calcified, are thick and extend farther anteriorly than the palatoquadrates, but do not extend as far posteriorly (Fig. 2.2). The dorsal part of each cartilage curves down slightly from posterior to anterior, and ends anteriorly in a rounded edge. This curvature is reinforced by a thickened ridge of cartilage (Fig. 2.2A).

The ventral part of each Meckel's cartilage is sharply curved in the posterior portion and flattens out for the anterior half. This anterior, flattened half of the cartilage is where the symphysis between the left and right Meckel's cartilages occurs (Fig. 2.2B). Due to the preservation of the two specimens with preserved heads, the angle and shape of the symphysis of these cartilages is unclear, but it is clear that the symphysis is very long (Fig. 2.2).

The ventral part of each Meckel's cartilage is also reinforced by a thickened ridge, which becomes thicker and more prominent posterior to the symphysis. Here, where the cartilage is angled dorsally, the ridge becomes thicker and more flange-like. This flange-like ridge continues up past the posterior end of the cartilage and becomes a pointed, triangular process that is assumed to play a part in the articulation between the palatoquadrate and Meckel's cartilages (Fig. 2.2B).

Additional Structures—There is no evidence for overlying bone, teeth, or other dentigerous structures associated with the rostrum or the oral cavity of *K. rosulentus*.

Class ACANTHODII Owen, 1846
Order DIPLACANTHIFORMES Berg, 1940
Suborder DIPLACANTHOIDEA Miles, 1966
Family GLADIOBRANCHIDAE Bernacsek and Dineley, 1977
Genus *GLADIOBRANCHUS* Bernacsek and Dineley, 1977
GLADIOBRANCHUS PROBATON Bernacsek and Dineley, 1977
(Fig. 2.3)

Revised Diagnosis—Small acanthodian with large gape; Meckel's cartilages ossified, shovel-shaped; palatoquadrate cartilages not ossified; lacking teeth, other dentigerous structures. For additional diagnostic features, see Hanke (2001:287-311).

Holotype—NMC 22700A.

Material—UALVP 19259, 38679, 41858, 41862, 42093, 47074, 47079, 47080.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—*Gladiobranchus probaton* (Fig 2.3A) was first described by Bernacsek and Dineley (1977:13-17) based on a partially preserved body fossil lacking much of the head, and the ossified Meckel's cartilages. Those authors also placed the family Gladiobranchidae, problematically, within the Ischnacanthiformes, assuming that they possessed dentigerous jaw bones, as well as drawing attention to a resemblance to *Uraniacanthus*. *Gladiobranchus probaton* was redescribed by Hanke (2001) based on multiple, almost complete specimens. Based on the increased number of specimens, as well as their magnificent preservation, *Gladiobranchus* has since been placed within the Diplacanthiformes. The following description focuses on the oral region of *Gladiobranchus probaton*. For a complete morphological description, see Hanke (2001:287-311).

Gladiobranchus probaton is a small diplacanthid acanthodian with a large mouth and naked rostrum. The only evidence of the gape of the mouth comes from the ossified Meckel's cartilages (Fig. 2.3A). The ossified cartilages have a texture similar to that of the endochondrally formed pectoral girdles of this species and other acanthodians, differing from that of the calcified cartilages in the putative chondrichthyans (see *Kathemacanthus rosulentus* above).

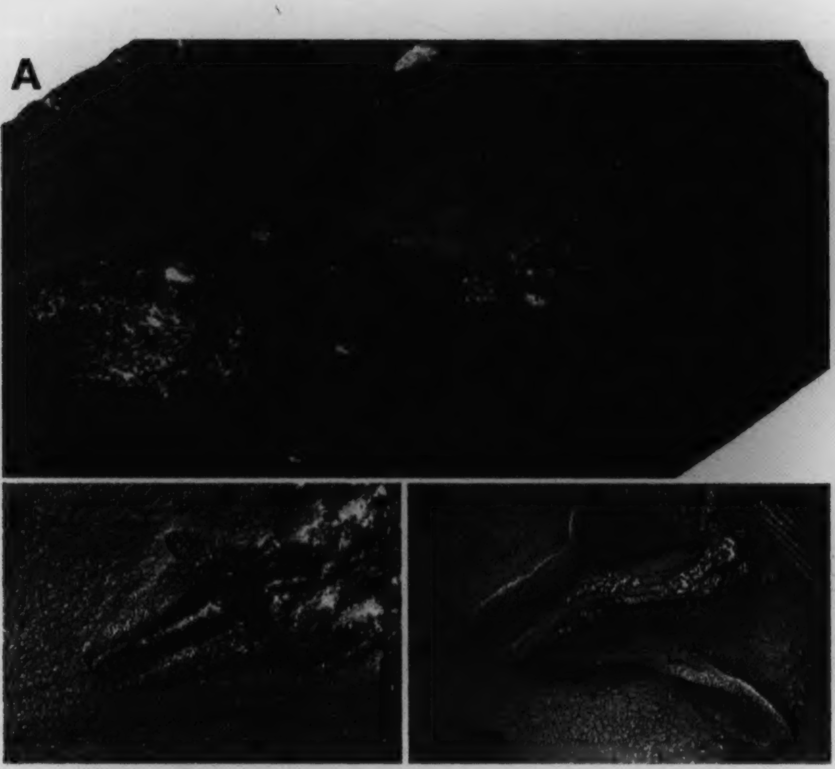

FIGURE 2.3. *Gladiobranchus probaton.* **A**, UALVP 41858, one of the most complete specimens of *G. probaton* showing preserved Meckel's cartilages; **B**, a close-up of the Meckel's cartilages of UALVP 41858; **C**, UALVP 47074, a close-up of the jaws of *G. probaton* showing the labial and lingual sides of the cartilages. Scale bar for **A** equals 1cm, all others equal 1mm.

Palatoquadrate Cartilage—There is no evidence of ossification of any part of the palatoquadrate in any of the specimens (Fig. 2.3A).

Meckel's Cartilage—In the UALVP collection, there is a great deal of size variation among the specimens of *Gladiobranchus probaton*. In all of the specimens with the head preserved, there is at least some preservation of the Meckel's cartilages. In the small, presumably younger specimens, the Meckel's cartilages are thin and not very robust. As the specimens increase in size, the cartilages increase in completeness and robustness. In the largest specimens, the Meckel's cartilages are completely ossified and more robust than is seen in the smaller, younger forms (Fig. 2.3B, C).

The Meckel's cartilages are long and wide, with a rounded anterior end. They extend from what is, presumably, the anterior part of the lower jaw, all the way posteriorly to a point underneath the beginning of the hyoidean gill covers (Fig. 2.3A, C).

The ventral edge is mostly straight, but has a slight upward curvature in the middle of the cartilage. In the larger specimens, this edge is reinforced by a thickened ridge of ossified cartilage (Fig. 2.3B).

Anteriorly, the edge of the tip follows a similar curvature to that of the bottom edge. A little past the middle of the cartilage, there is a large, rounded process extending dorsally; this process takes up about a quarter of the top edge of the cartilage. Posterior to this process, the curvature of the dorsal edge once again parallels that of the ventral edge, with the cartilage at the posterior end of the

Meckel's cartilage being only slightly deeper (taller) than what was seen anteriorly. Like the ventral edge, the dorsal edge is also reinforced by a thickened ridge of ossified cartilage (Fig. 2.3C).

The centers of the Meckel's cartilages are thinner than the outside edges and are best preserved in the larger, older specimens. This middle portion is pinched concavely inward along the extent of the cartilage from anterior to posterior. In lingual view, it can be seen that this pinching is actually caused by a thick ridge of cartilage that extends up into the rounded process on the dorsal edge of the cartilage. Under this thickened area of cartilage, the curvature of the thinner ventral edge can be seen (Fig. 2.3C).

From this view, it can also be seen that the entire cartilages curve inward as well. This reinforced area is confusing and its function is unclear. It may be a symphysis of the lower jaws, but it does not seem functional. This long area of inward curving of the Meckel's cartilages gives the lower jaw the appearance of a trough or shovel (Fig. 2.3B, C). It is assumed that this structure would have aided in feeding and that this style of feeding would have been consistent throughout ontogeny because the jaws change relatively little in shape and growth.

There is no evidence of how the Meckel's cartilages would have articulated with the palatoquadrate cartilages. I believe that it is possible that only the more anteroventral portion of the Meckel's cartilages are preserved and that the upper, articulating part was not ossified, and therefore not preserved (similarly to the palatoquadrate).

Additional Structures—There is no evidence of overlying bone, teeth, or other dentigerous structures associated with the rostrum or the oral cavity of *G. probaton* (Fig 2.3A).

Family TETANOPSYRIDAE Gagnier et al., 1999

Revised Diagnosis—Revisions based on the structures of the oral cavity; for a complete diagnosis, see Hanke et al. (2001:742). Palatoquadrate and Meckel's cartilages ossified; broad, flattened bony plates overlying upper and lower cartilages.

Genus *TETANOPSYRUS* Gagnier et al., 1999

Revised Diagnosis—Diagnosis based on structures of the oral cavity; for complete diagnosis, see Hanke et al. (2001:742). Articulation between upper and lower jaws strong (but exact form and function still unclear); upper bony plates overlapping/occluding broadly over lower bony plates.

Revisions to the Description—The jaws of *Tetanopsyrus* have a common form of overlapping bony plates supported by the ossified Meckel's and palatoquadrate cartilages (Figs. 2.4, 2.5). Overall, these cartilages have a smooth texture, resembling that of the endochondrally formed pectoral girdles in various species of acanthodians. It is very possible that these cartilages were formed similarly to those seen in *Gladiobranchus probaton* and the other acanthodians discussed in this chapter, differing from the globular calcified cartilage seen in

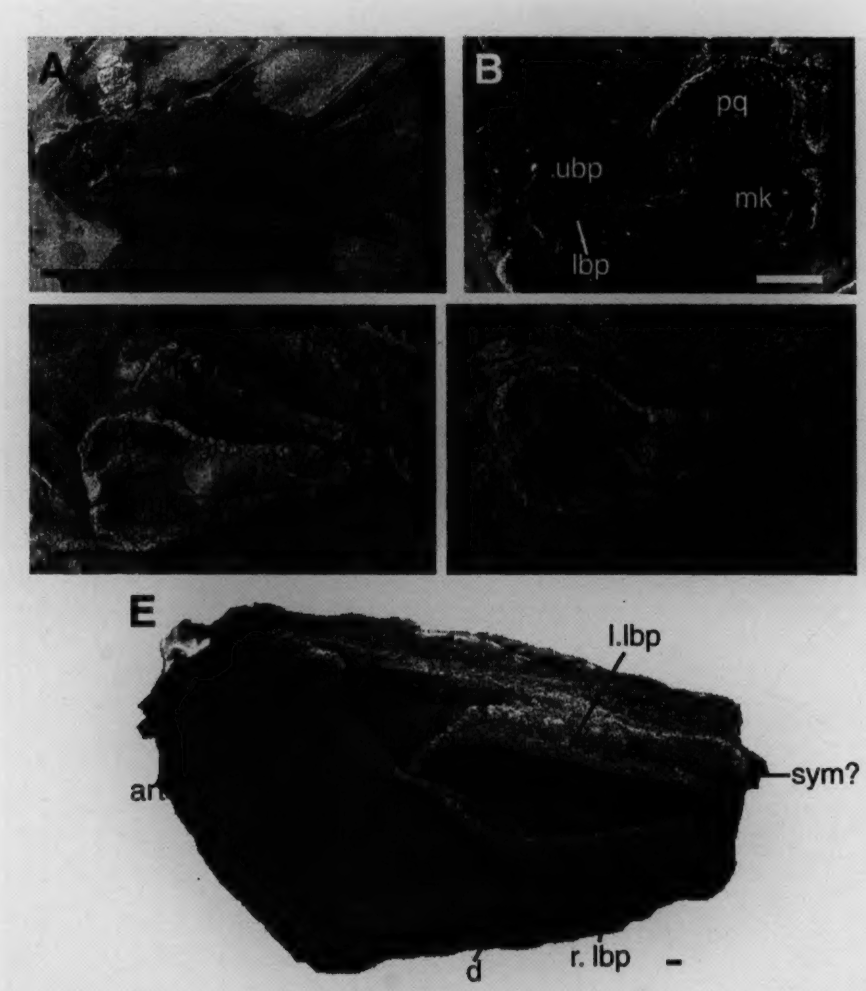

FIGURE 2.4. *Tetanopsyrus lindoei*. **A**, UALVP 32571, the most complete specimen of *T. lindoei*, with **B**, a close-up of the cartilages and bony plates; **C**, UALVP 39078, the left and right jaws of the holotype of *T. lindoei*; **D**, UALVP 43026, right jaws with the posterior portion of the lower bony plate broken off, showing a possible denticulated surface; **E**, UALVP 47085, two lower jaws (in labial view) showing denticulated surfaces. Scale bar for **A** equals 1cm, scale bars for **B**-**D** equal 1mm, scale bar for **E** equals 100 um.

some of the putative chondrichthyans (see *Kathemacanthus rosulentus* above; Fig 2.2).

There is a great deal of difference between the 'jaws' of the two known species; the differences include shape of the cartilages and overlapping bony plates, as well as the presence or absence of tooth-like denticulations on these plates. The differences between the jaws of these two species are great enough that these new characteristics are diagnostic features that can be used to differentiate the two species. The differences are described below.

TETANOPSYRUS LINDOEI Gagnier et al., 1999

(Fig. 2.4)

Revised Diagnosis—Diagnosis based on features of the oral cavity; for complete diagnosis, see Hanke et al. (2001:742). Cartilages and overlying bony plates, with scissor-like appearance; palatoquadrate L-shaped; tooth-like denticulation on labial surface of lower bony plates; bony plates square posteriorly.

Holotype—UALVP 39078.

Referred Material—UALVP 32571, 38682, 43026, 47078, 47085.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—Due to an increased number of excellent specimens, as well as giving close attention to the detail of the upper and lower jaws of *Tetanopsyrus lindoei* (Fig. 2.4), certain diagnostic features of the species can be suggested. The cartilages are large, robust, ossified, and support bony plates. The combination of the ossified cartilages and overlying bony plates comprises the jaw complex. The bony plates overlying the cartilages are long, smooth and rounded, and at least the lower plates have a row of denticulations. The cartilages are well preserved and the articulation point between the palatoquadrate and Meckel's cartilages can be clearly seen. The combination of the cartilages and overlying bony plates gives the jaw apparatus a scissor-like appearance (Fig. 2.4B-D).

Upper Jaw: Palatoquadrate Cartilage—The palatoquadrate cartilage is ossified and supports the large, upper bony plate. Posteriorly, the cartilage is semi-circular and becomes elongate and thin where it supports the bony plates (Fig. 2.4B, C).

The shape of the palatoquadrate, as well as where the bony plate overlaps it, is seen in the holotype of *T. lindoei*, UALVP 39078 (Fig. 2.4C). The posterior portion of the ossified cartilage is semi-circular. Immediately posterior to where the bony plate overlies the cartilage, the margin of the cartilage descends, and the cartilage becomes thinner where it supports the plate.

On the posterior, ventral edge of the ossified palatoquadrate, there is a long, oval process pointing ventrally, articulating with the Meckel's cartilage.

The process is more robust than the rest of the cartilage and projects laterally (Fig. 2.4C).

Upper Jaw: Bony Plates—The upper bony plates are smooth and long, and completely cover the long, thin anterior part of the palatoquadrate cartilage. These upper plates occlude over most of the width of the lower bony plates, and also extend anteriorly beyond the lower plates. Each upper plate sits on the medio-labial part of the palatoquadrate (Fig. 2.4B-D).

In all of the specimens of *T. lindoei*, the upper bony plates are rounded laterally along their labial edges. Anteriorly, this rounded shape ends and the bony plate flattens out and tapers slightly towards the front of the mouth (Fig. 2.4B, C).

The top of each bony plate is flat and the plate is rounded at its anterior tip. The plates maintain the same thickness throughout their length and do not show any growth zones. The bottom edge of the plate is straight and smooth and this aspect does not change along the length of the plate (Fig. 2.4B-D).

Due to the nature of the preservation of the jaws (in body fossils, the upper bony plates are always occluded on top of the lowers), the outer surface of the bony plates is always what is exposed (Fig. 2.4B-D). As yet, I have not found any specimens of isolated upper jaws that could be removed and provide a view of the lingual side of the upper plates. Therefore, I cannot be sure if the lingual edge of the upper bony plate is denticulated like the lower plate (see description below). I do suspect that this is the case as the occlusion of the upper and lower plates would also form a shearing surface.

Lower Jaw: Meckel's Cartilage—The Meckel's cartilage is large, ossified, and has an overall, inverted L-shape, with a large articulation surface and other processes to aid in the attachment to the palatoquadrate (muscle, etc). The posterior portion is flat and broad with associated flanges. The lower, more posterior flange has been interpreted as the articulation point with the palatoquadrate; the upper, slightly anterior flange is interpreted as functioning for muscle attachment (Fig. 2.4C, E).

The posterior ventral edge of the cartilage is rounded and the cartilage flattens out anteriorly. The dorsal edge of the Meckel's cartilage slopes down from the high flange and flattens out to make the upper edge of the anterior part of the cartilage. The anterior part is long and narrow, and is about the same length as the posterior portion. It terminates anteriorly in a rounded edge (Fig. 2.4E). There is no clear evidence for a strong symphysis between the left and right Meckel's cartilages. Most of the morphology of the anterior part of the cartilage is obscured by the overlying bony plates (Fig. 2.4B-D).

The posterior part of the Meckel's cartilage of *T. lindoei* is the best-known and understood part of the cartilages of this genus. This is due to the discovery of a pair of isolated lower jaws, UALVP 47085 (Fig. 2.4E). In body specimens, these cartilages are usually in articulation with the palatoquadrate as well as covered by head scales. Also, in all of the specimens assigned to this genus, the anterior portion is partially or fully covered by the overlying bony plate.

Hanke et al. (2001) labeled processes and articulation points on an isolated pair of lower jaws, unnumbered and identified only to *Tetanopsyrus* (Fig. 3B in Hanke et al., 2001). The lower jaws have since been removed, imaged with the SEM and given the number UALVP 47085. I believe that the articulation process of the Meckel's with the palatoquadrate is not where Hanke and the coauthors labeled it, but rather at what he labeled the articular cotylus (art.c.) and that what was labeled as the articulation with the palatquadrate (art.pq.) aided in muscle attachment. Unfortunately, due to the lack of exposed lower jaws, this idea is hard to verify. On UALVP 47085, there is no evidence for muscle scarring to understand better the upper jaw to lower jaw articulation (Fig. 2.4E).

This new interpretation of the points of articulation between the palatoquadrate and Meckel's cartilages may help to understand better how *T. lindoei* might have used its jaw complex. This interpretation may also solve the lock-jaw problem, after which the genus was named (see Gagnier et al., 1999), whereby earlier researchers could not understand how the jaws were able to articulate movably in life.

Concerning the same specimen, UALVP 47085, Hanke et al. (2001) had determined that the specimen was "a pair of isolated *Tetanopsyrus* lower jaws visible in medial view." I think it is much more parsimonious to interpret the specimen as two lower jaws seen in lateral view, placing the denticulated surfaces on the labial (outside) surfaces of the lower jaws. This idea can be supported by looking at the two lower jaws and imagining how they would have been preserved. Assuming that the two jaws were attached at a symphysis near their anterior-most points, it is most likely that during disarticulation, the jaws fell inwards and slightly overlapped. If this were the case, we should be looking at the labial sides of the lower jaws. For the jaws to be preserved in medial view, as Hanke et al. (2001) described, the jaws would have had to fall outward, and then rotate towards each other and overlap to be preserved in their fossilized state (Fig. 2.4E).

Unfortunately, UALVP 47085 is the only specimen in which the lower jaws are isolated. Possible future thin sectioning or small scale CT scanning could aid in a better understanding of these structures.

Lower Jaw: Bony Plates—As in the upper jaws of *T. lindoei*, there is a bony plate that covers most of the anterior portion of its supporting cartilage, in this case the Meckel's cartilage. In most cases, these bony plates are mostly covered by the occluding upper bony plates. In two specimens, UALVP 47085 (Fig. 2.4E) and 43026 (Fig. 2.4D), the bony plate is exposed fully or partially, respectively, allowing a better understanding of the morphology and possible function of these plates.

As described above, UALVP 47085 consists of a pair of left and right unarticulated lower jaws. These jaws were fossilized in lateral view, fully exposing the bony plates. The bony plates can be distinguished from their underlying ossified cartilages by noting their increased thickness, and the row of denticulation along their lingual edges (Fig. 2.4E).

This denticulation consists of a single row of raised, rounded cusps of similar size. The precise pattern and morphology of the cusps is difficult to determine, most likely due to weathering of the specimen. Oddly, the row of denticulation is along the labial edge of the bony plate and is directed towards the bottom of the jaw complex (Fig. 2.4E).

UALVP 43026 is a full body specimen with the jaws preserved in situ. This specimen is important, because a part of the occluding upper bony plate is broken off, exposing the posterior portion of the lower bony plate. On this exposed portion, the downward-facing denticulation can be seen (Fig. 2.4D). This specimen helps to confirm that UALVP 47085 is seen in lateral view, as well as that it belongs to *T. lindoei*.

Remarks—The position of the denticulation on the lower bony plates of *T. lindoei* is puzzling. Due to the rarity of specimens and more particularly the lack of sectionable/destroyable specimens, I cannot be sure how these denticulations may have functioned during the life of the acanthodian.

It is possible that the upper jaws also possessed a similar type of dentition on their bony plates, in this case directed dorsally, towards the top of the palatoquadrate cartilage. When the two plates occluded, they might have made a crushing surface. This is only a hypothesis and would need to be tested via small-scale CT-scanning and by thin-sectioning. Thus far, there has been no external evidence found of growth zones or other possible modes of growth of the jaw complexes.

TETANOPSYRUS BREVIACANTHIAS Hanke et al., 2001

(Fig. 2.5)

Revised Diagnosis—Diagnosis based on features of the oral cavity: for complete diagnosis, see Hanke et al. (2001:743). Cartilages and overlying bony plates ossified giving duck-billed like appearance; palatoquadrate cartilages large, covering most of the Meckel's cartilages; no denticulation or tooth-like structures on labial side of bony plates; bony plates triangular posteriorly.

Holotype—UALVP 43246.

Referred Material—UALVP 42114, 42512, 43089, 44030, 45153, 48618.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—Based on new specimens and a focus on their dentitions, *Tetanopsyrus breviacanthias* can be easily distinguished from *Tetanopsyrus lindoei*. The jaw complex of *T. breviacanthias* has a duck-billed like appearance, where only the palatoquadrate cartilage is visible or distinguishable. The degree of ossification of the cartilages is also a differentiating factor; in general, those of *T. lindoei* appear much more solid and robust than those of *T. breviacanthias*. The bony plates are also not as robust as seen in *T. lindoei*, and the upper bony plate occludes almost completely over the lower bony plate. The overall shape of the bony plates also varies between the two species. The plates in *T. breviacanthias* terminate posteriorly in a point, or spur, and are therefore not rectangular like those of *T. lindoei* (Fig. 2.5).

Palatoquadrate and Meckel's Cartilages—In *Tetanopsyrus breviacanthias*, the palatoquadrate and Meckel's cartilages are very difficult to distinguish from one another. The anterior portions of the cartilages are completely covered by their corresponding overlying bony plates.

The posterior part of the cartilage is circular, giving the jaw complex a duck-billed appearance. It is my guess that the majority of the posterior circle of cartilage seen in the specimens is formed by the palatoquadrate cartilage, with the Meckel's cartilage mostly nearly totally obscured (Fig. 2.5B). There is no evidence indicating the type of articulation between the upper and lower jaws (Fig 2.5).

Upper Jaw: Bony Plate—The upper bony plate of *Tetanopsyrus breviacathias* is long and smooth and completely covers the anterior part of the palatoquadrate. As in *T. lindoei*, the upper bony plates do not have a definite symphysis between the left and right components (Fig. 2.5A).

Unlike the condition in *T. lindoei*, the bottom part of the upper bony plate extends posteriorly past the upper part. This gives the posterior portion of the

FIGURE 2.5. Jaws of *Tetanopsyrus breviacanthias*. **A**, UALVP 43246, the right jaws of the holotype of *T. breviacanthias*; **B**, the right jaws of UAVLP 42512, showing the duck-billed shape of the jaws. Scale bars equal 1mm.

upper bony plate a triangular end, making this a distinguishing characteristic of this species (Fig. 2.5A).

Lower Jaw: Bony Plate—Little information has been gathered about the lower bony plate of *T. breviacanthias*. In all of the specimens in the UALVP collection, the jaw complexes are complete with upper and lower jaws preserved closed. In this position, the upper bony plate occludes mostly if not completely over the lower bony plate (Fig. 2.5), hiding any distinguishing features (Fig 2.5).

In the holotype of *T. breviacathias*, UALVP 43246 (Fig. 2.5A), the most ventral part of the lower bony plate is exposed. From this it appears that the lower bony plate extends as far posteriorly as the upper bony plate, but does not extend as far anteriorly.

For a better understanding of the morphology of the lower bony plate of *T. breviacanthias*, isolation and removal of the lower jaw component would be necessary. Thin sectioning and small-scale CT-scanning may also help to understand better this structure.

Remarks—There are multiple specimens identified as juvenile forms of *T. breviacanthias* (Hanke, 2001) that should be examined in more detail to look for ontogenetic changes in jaw development. This may give more insight into how these jaw complexes grew and developed and whether different parts developed at different times during ontogeny.

Based on the new information about the differences between the two species of *Tetanopsyrus*, the two species can be distinguished based on isolated jaw elements. This will be useful for identification of isolated or partially preserved specimens of *Tetanopsyrus*.

Gen. Nov. A et sp. nov. A

(Figs. 2.6-2.7)

Diagnosis—Diplacanthid acanthodian within the Tetanopsyridae based on isolated upper and lower jaws; palatoquadrate and Meckel's cartilages ossified, posteriorly rounded, tapering to a thin bar anteriorly; no clear articulation between upper and lower jaws; bony, denticulated plates overlying palatoquadrate and Meckel's cartilages; one or more rows of rounded, not deeply ankylosed teeth.

Material—UALVP 47239.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—The only specimen of Gen. Nov. A et. sp. nov. A (UALVP 47239) consists of the upper and lower jaws, comprised of bony plates sitting on their respective palatoquadrate and Meckel's cartilages (Figs. 2.6A, 2.7B). The bony plates have rows of denticulations. The cartilages are at least partially ossified, and have a slightly different texture than the bony plates. Unfortunately the only specimen of this species is partially damaged from weathering and can only give limited information.

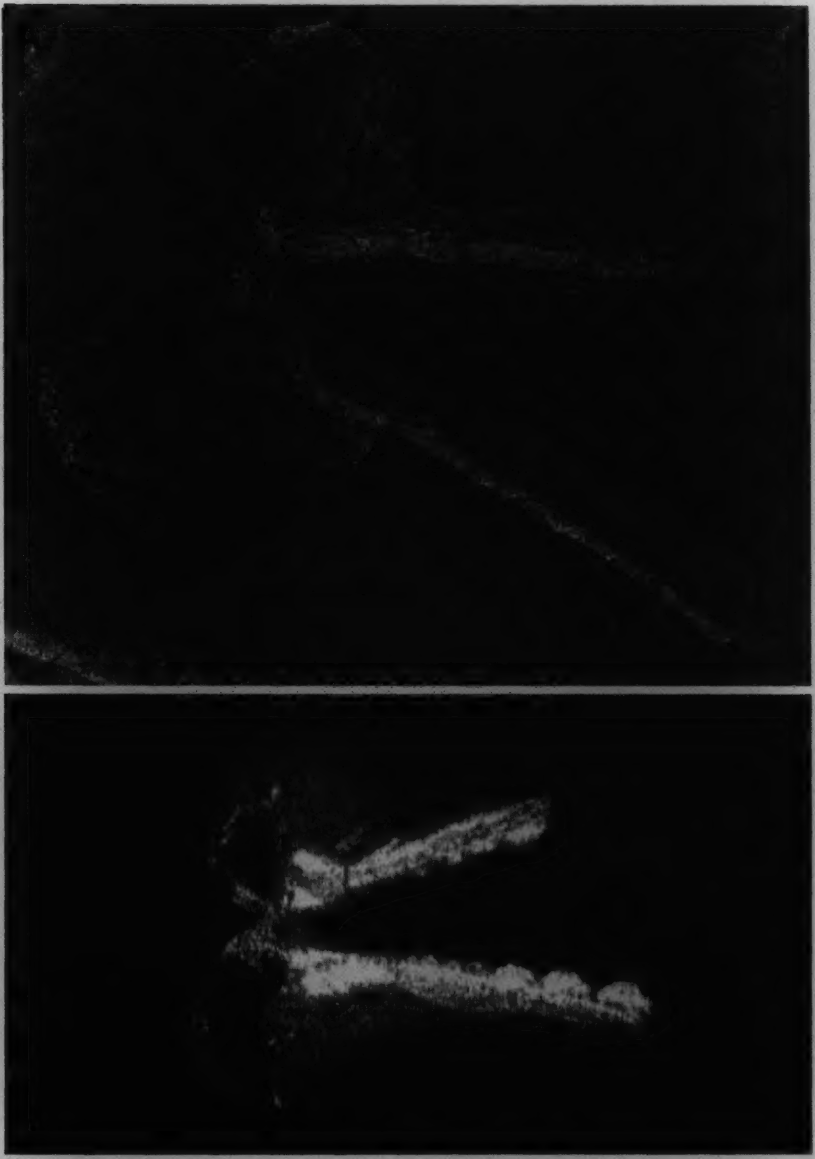

FIGURE 2.6. Gen. Nov. A et sp. nov. A., UALVP 47239. **A**, right upper and lower jaws; **B**, small-scale CT-scan through the upper and lower jaws, there is no evidence for a solid pulp cavity and the teeth are not deeply rooted like in Ischnacanthids (scale bar estimated). Scale bars equal 1mm.

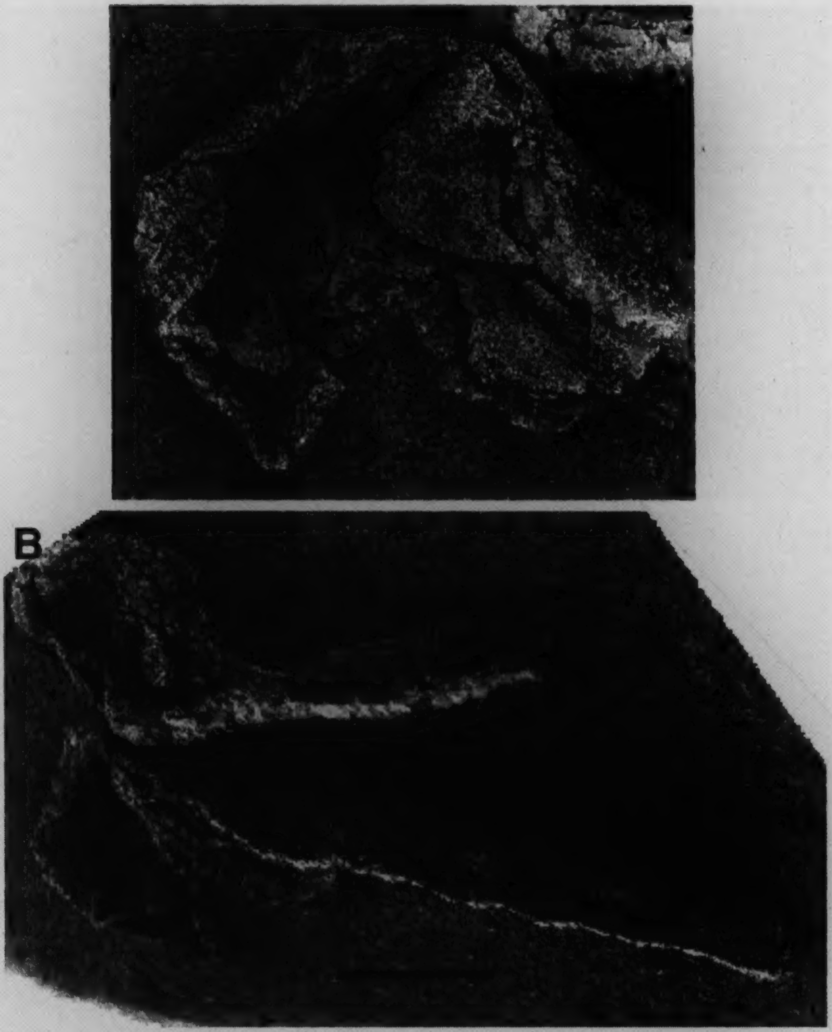

FIGURE 2.7. Gen. Nov. A et sp. nov. A. **A**, close-up of the lower jaw where the bony plate overlies the Meckel's cartilage; **B**, oblique view of the jaws showing the denticulated surface of the lower bony plate. Scale bar for **A** equals 100um, scale bar for **B** equals 1mm.

Palatoquadrate and Meckel's Cartilages—Both the palatoquadrate and Meckel's cartilages are obscured anteriorly by their corresponding bony plates. Posteriorly, the cartilages are circular and they taper quickly to a thin bar anteriorly, where they are covered by the bony plates (Fig. 2.6A).

Due to the preservation of the specimen, it is difficult to tell whether the bony plates mostly or completely cover the cartilages. Based on the small-scale CT data (Fig. 2.6B), it does appear that a small portion of the cartilage is exposed (light grey versus white portions).

Upper Jaw: Bony Plate—Much of the upper bony plate of Gen. Nov. A et sp. nov. A was damaged by weathering. The length facing out of the rocks was severely weathered and the anterior edge of the plate was broken off Fig 2.6A, 2.7A).

The bony plate extends from near the posterior part of the palatoquadrate all the way to the anterior of the cartilage. On the upper bony plate, there is at least one row of rounded teeth, increasing in size anteriorly. The teeth do not begin as far posteriorly on the upper bony plate as they do in the lower bony plate, but do increase in size anteriorly (Fig. 2.6A).

Lower Jaw: Bony Plate—The bony plate of the lower jaw is mostly preserved, but the edge facing labially appears to have been slightly broken, most likely due to wear of the exposed surface on the talus slope. The bony plate begins near the posterior end of the ossified Meckel's cartilage and extends slightly past its anterior end. The posterior edge of the bony plate is broad and extends farther ventrally than down from the rest of the plate (Fig. 2.6A).

On the dorsal edge of the bony plate, there are four rows of low, rounded teeth. The teeth are monocuspid and are rounded to sub-rounded in shape. All of the teeth are similar in morphology and they increase in size anteriorly (Fig 2.6A, 2.7B).

The largest row is the main row and has eleven tightly packed teeth. These teeth increase in size anteriorly. This row extends from the back of the plate to the anterior edge. The teeth increase dramatically in size at the point where this row becomes the only persisting row of teeth (Fig. 2.7B).

There are three more medial rows of teeth that do not extend the entire length of the bony plate, and therefore have much smaller cusps. The medial row closest to the main row is the longest, with six teeth: the middle row has five teeth and the outer-most row has four teeth (Fig. 2.7B).

Internal Structures—I was able to small-scale CT-scan the only specimen of Gen. Nov. A et sp. nov. A (Fig. 2.6A). The resolution obtained was not as good as I had hoped, but I still obtained some information about the internal structures.

The bony plate appears to be vascularized with a series of networked canals. There is no evidence of growth zones in the bony plate to indicate how the structure grew over time.

The teeth on the bony plate are rounded and are vascularized by a series of canals, instead of a single pulp cavity like that seen in the Ischnacanthidae (see below). The connections between the vascular canals in the teeth and those in the bony plates are unclear. The teeth are not deeply inserted into the bony plates but appear to sit more on the top surface of their associated plates (Fig. 2.6B).

Remarks—Gen. Nov. A et. sp. nov. A has been placed within the Tetanopsyridae due to the similarity of the jaw complex (combination of cartilages and corresponding bony plates) of this species to those seen in the two species of *Tetanopsyrus* (see above descriptions). In all three species there are denticulated bony plates overlying the Meckel's cartilage. Because of these similarities, and due to the lack of more fossil evidence, I feel comfortable placing this new species within the family Tetanopsyridae. A comparison of the histology of the two species of *Tetanopsyrus* and Gen. Nov. A et sp. nov. A would be a good way to test for a close association between these taxa. More, better preserved specimens will help to increase our knowledge and placement of this new species.

Order ISCHNACANTHIFORMES Berg, 1940
Family ISCHNACANTHIDAE Woodward. 1891
Genus *ISCHNACANTHUS* Powrie, 1864
(Figs. 2.8-2.11)

Diagnosis—Based on the preliminary descriptions by Hermus (2003). Diagnosis limited to dentigerous jaws identified to genus *Ischnacanthus*. Palatoquadrate and Meckel's cartilages ossified, with associated overlying dentigerous bony plates ('jaw bones'); palatoquadrate large, semicircular; Meckel's cartilage semi-oval in shape; cartilages extending anteriorly beyond overlying bony plates; single point of jaw articulation; bony plates with one or more rows of teeth; teeth deeply socketed/ankylosed to jaws.

Material—Jaw bones: 32520, 39063, 41527, 42036, 42062, 42596, 43257, 43994, 45038, 45075, 45087, 45548, 45620, 47113, 47222, 47234, 47237; jaw bones with preserved cartilages: 19261, 19267, 23294, 32401, 32405, 32414, 32443, 32447, 32470, 39058, 39060, 39086, 39120, 41491, 41650, 41663, 41920, 41929, 42015, 42055, 42143, 42183, 42198, 42199, 42201, 42202, 42203, 42214, 42520, 42658, 42659, 42660, 42661, 42664, 43245, 44027, 45014, 45034, 45035, 45037, 45039, 45040, 45072, 45073, 45074, 45076, 45077, 45078, 45079, 45080, 45081, 45082, 45097, 45553, 45648, 45650, 47082, 47094, 47117, 47216, 47223.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—This study focuses on the dentition based on the genus *Ischnacanthus* (Fig. 2.8), without looking at specific morphologies based on different species (a study focusing on the different species of *Ischnacanthus* at the MOTH locality has already been conducted; see Hermus

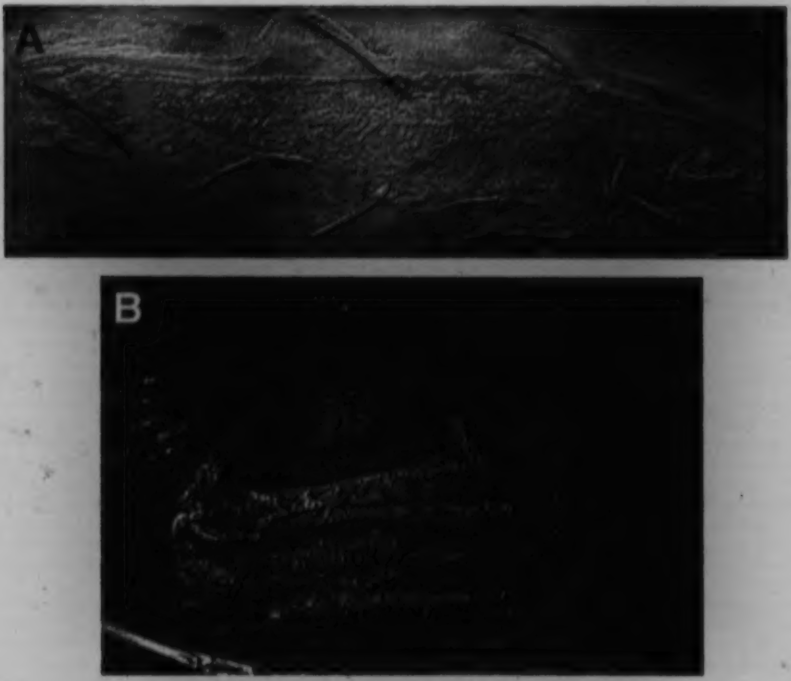

FIGURE 2.8. UALVP 45014, *Ischnacanthus* sp. **A**, full body specimen, in right lateral view, preserved with complete upper and lower jaws; **B**, close-up of the upper and lower jaws, showing the upper and lower cartilages, their overlying plates and articulation point. Scale bars equal 1cm.

[2003]). There will be a focus on the general morphology and histology of the jaws in relation to growth of and possible addition of teeth to the bony plates.

The jaws consist of ossified palatoquadrate and Meckel's cartilages with overlying dentigerous, bony plates. The cartilages are large and thick, and are reinforced on their labial edges by a thicker band of cartilage (it is unclear if this band is extended beneath the bony plates) (Figs. 2.8B, 2.9). Watson (1937) suggested that there were at least 2 points of calcification in the palatoquadrate and Meckel's cartilages; there is no evidence for this in any of the UALVP specimens. The texture of the cartilages resembles that of the ossified pectoral girdles, not that of the calcified cartilages in *Kathemacanthus rosulentus* (see above).

In some cases, the cartilages are not preserved and only the bony plates are present (Fig. 2.10). It is unclear if this is a factor of preservation or if this is an ontogenetic change. It is most likely that this is a preservational bias instead of a morphological one, because most of the specimens studied (78%) had preserved cartilages. The size of the specimens studied varied greatly but there is no consistent relationship between the size of the bony plate and presence or absence of ossified cartilage.

There is a single point of articulation between the upper and lower cartilages, located posteriorly. The Meckel's cartilage has a small, rounded process that fits into a corresponding concave surface on the back of the palatoquadrate (Figs. 2.8B, 2.9).

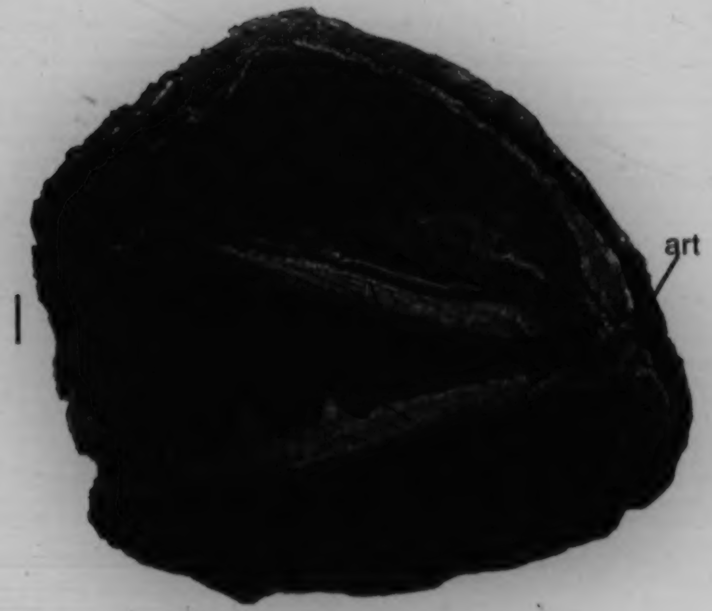

FIGURE 2.9. *Ischnacanthus* sp., assembled SEM images of isolated upper and lower jaws of UALVP 47223 (seen in lateral view); note how the bony cartilages and corresponding bony plates become fused, as well as how the cartilages extend anteriorly in front of the overlying bony plates. Scale bar equals 1mm.

In both the upper and lower jaws, the cartilages extend anteriorly, beyond the ends of the bony plates (Figs. 2.8B, 2.9). This could allow an area of attachment for the symphyseal tooth whorls (Fig. 2.9; see Chapter 3), or it could be an area for future growth of the bony plates. The exact means of growth of the bony plates is still very unclear and future comparative morphological and histological work needs to be done to clarify it.

Upper Jaw: Palatoquadrate Cartilage—The palatoquadrate cartilage in *Ischnacanthus* is massive and semi-circular in shape. The semi-circle is slightly asymmetrical; the tallest part of the cartilage is anterior to the center, usually near where the anterior edge of the bony plate sits (Fig. 2.9).

The outer edge of the cartilage is reinforced by a thickened band of cartilage. This band is largest posteriorly, near the articulation with the Meckel's cartilage. Anteriorly, the band is still present but is much smaller and harder to identify in some of the specimens (Fig. 2.8B). This area could be where the cartilage is increasing in size ontogenetically to accommodate more, larger teeth.

On the bottom part of the palatoquadrate cartilage sits one of the bony plates. The bony plates contain a groove-like concavity, to fit over the cartilages. Besides this, the morphology of the cartilage under the bony plate is unclear; there are no specimens with ossified cartilages but missing dentigerous bony jaws.

There is no clear articulation point between the left and right palatoquadrates (Fig. 2.8B). It is most likely that there was little, if any articulation between the two sides. If there were, it would probably be at a small

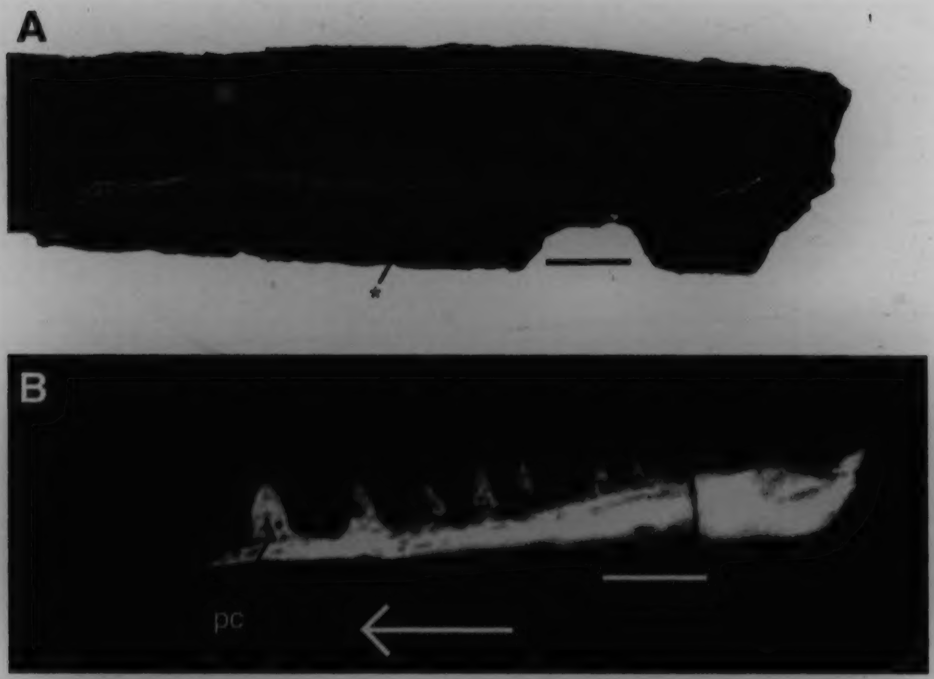

FIGURE 2.10. UALVP 47117, *Ischnacanthus* sp. **A**, isolated bony plate in side view (it is unclear if this is an upper or lower jaw element); note how the teeth increase in size anteriorly, the star indicates where the bony plate would overlie the corresponding cartilage; **B**, small-scale CT-scan through the center of the jaw showing the hollow pulp cavity of the tooth and how the teeth extend farther into the bony jaw than would be expected based on external morphology (scale bar estimated). Arrows point anteriorly. Scale bars equal 1mm.

point, not a large area, and possibly farther anteriorly where the cartilage is not ossified.

At the posterior, ventral edge of the palatoquadrate there is a small, concave surface. This is the area where the process of the Meckel's cartilage articulates with the palatoquadrate (Figs. 2.8B, 2.9). This is the only point of articulation in *Ischnacanthus*.

Lower Jaw: Meckel's Cartilage—The Meckel's cartilage is smaller, and more semi-oval in shape than the palatoquadrate. Like the palatoquadrate, the Meckel's cartilage is asymmetrical, but in this case, the tallest part is focused posteriorly on the cartilage; this may be associated with the location of the process for articulation with the palatoquadrate and/or the area of insertion of jaw muscles.

The Meckel's cartilage extends anterior to its associated bony plate and in many cases extends anteriorly beyond the palatoquadrate cartilage. The cartilage tapers anteriorly and terminates in a slender point. As with the palatoquadrate, there is a thickened band of cartilage surrounding the outer edge of the Meckel's cartilage. This band is very thin or nonexistent near the anterior termination. As with the palatoquadrate, there is no evidence for symphyseal articulation of the Meckel's cartilages (Fig. 2.9).

At the dorsal, posterior edge of the Meckel's cartilage there is a small process that extends up towards and articulates with the palatoquadrate. The process is elongate with a rounded edge and fits into the concave surface on the palatoquadrate (Figs. 2.8B, 2.9).

Overlying Bony Plates—The overlying bony plates (usually referred to as 'jaw bones,' Ørvig, 1973) have elongate, groove-like concavities, which fit over their associated cartilages (Fig. 2.10A). In all of the observed specimens with preserved cartilages, the bony plates do not extend near the symphysis of the jaws. Posteriorly, the plates extend to just anterior to the articulation point. The dentition on the plates is oriented vertically up or down, depending on whether the plate is lower or upper, respectively (Figs. 2.8, 2.9).

The upper and lower plates themselves do not occlude over or overlap each other as seen in *Tetanopsyrus*, but when the jaws are closed, the main, lateral rows of teeth fit tightly beside and against each other (Fig. 2.8).

The morphology of the teeth varies dramatically among the different species (see Hermus, 2003), which are still formally undescribed, but there are consistent patterns throughout the genus. The bony plates have multiple rows of teeth, usually one lateral row with one or more medial, lingual rows, and teeth that increase in size anteriorly (Fig. 2.10). The largest teeth are always found in the lateral row.

In most of the specimens, there is also a morphological change in the teeth from the posterior to the anterior of the bony plates. This change can be very subtle (cusps less pointed to more pointed) or dramatic (older teeth are monocuspid, low and rounded, whereas newer teeth are multicuspid and more pointed) (Figs. 2.9, 2.10A). It has been suggested that this change is due to wear of the cusps, based on the way the teeth interlock in opposing jaws (Ørvig, 1973). However, there is no evidence for wear in any of the teeth on the dentigerous bony plates in the UALVP collection (Hermus, 2003, this study); this is supported by thin-section analysis (Fig. 2.11).

On the labial side of the bony plates, there are parallel ridges that extend along the length of the bony plates at an oblique angle. These ridges, along with the lack of medial rows of teeth, indicate the labial versus lingual side of the jaws in isolated specimens (Fig. 2.9).

In specimens of isolated bony plates of *Ischnacanthus*, we are able to tell the labial from the lingual side, but not an association with the upper or lower jaw. The bony plates are essentially identical in the upper and lower jaws, and because they do not participate in the jaw articulation, it is impossible to know from which jaw they came (Fig. 2.10A).

Based on the external morphology of the bony plates, there is no evidence indicating how they grew and how, or if, they added new teeth. In fact, Hermus (2003) suggested that they might not have added new teeth during growth, but that the existing teeth grew throughout life, because she found small and large specimens of the same species had the same number of teeth. As yet, I have found no evidence of this growth in the histological data.

Internal Structures—I have small-scale CT-scanned an isolated bony plate and completed thin-section work on two jaws of *Ischnacanthus* to look for

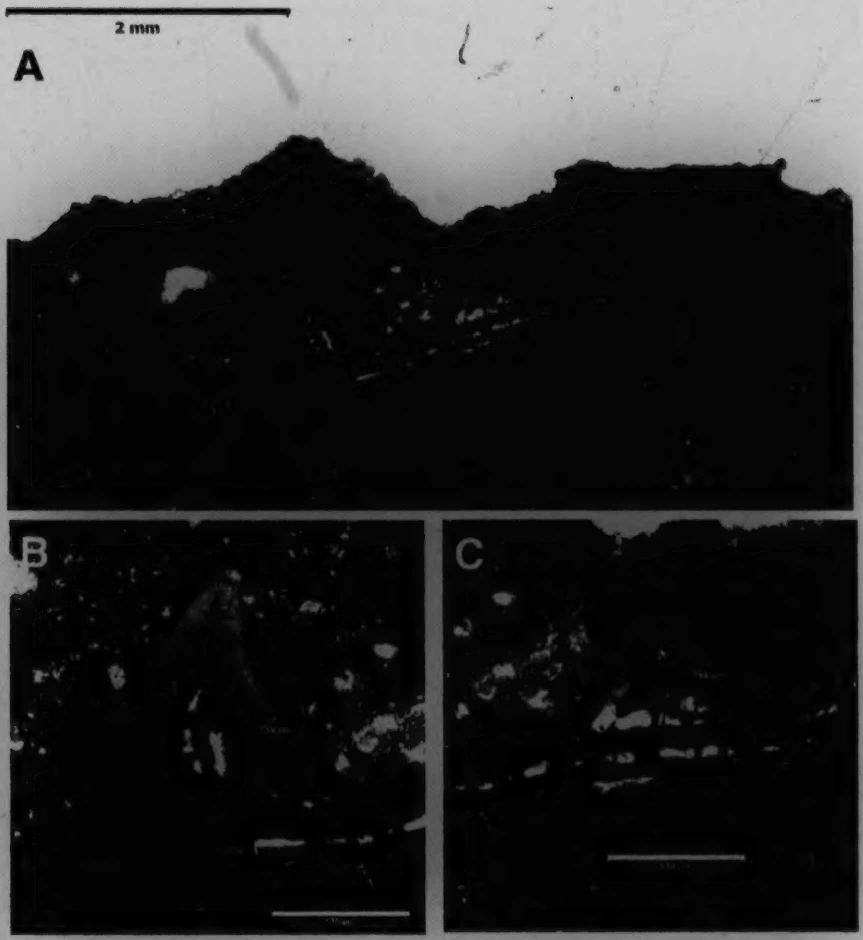

FIGURE 2.11. UALVP 32437, thin-section of dentigerous bony plate of *Ischnacanthus* sp. **A**, entire dentigerous bony plate, note the continuous layer of orthodentine over all of the tooth crowns (left is anterior); **B**, close-up of second largest tooth, white bar denotes orthodentine thickness of 76um; **C**, close-up of fourth largest tooth, white bar denotes orthodentine thickness of 66um. Scale bar for **A** equals 2mm, all other scale bars equal 200um.

histological details. Although the resolution was not as clear as hoped, it can be seen that each tooth has a single, hollow pulp cavity, similar to what is seen in the tooth whorls of this genus. From these scans it is unclear as to how these pulp cavities were connected and if there is a network of canals in the bony base (Fig. 2.10B).

It is also apparent and surprising that the teeth on the bony plates are deeply inserted into the bone. When comparing CT-data (Fig. 2.10A) to the actual specimen (Fig. 2.10B), the teeth appear to be small externally, but in the scans it is clear how far into the bony plate they extend. It is also clear from the scans that there is a separation between the teeth and the rest of the base of the dentigerous plate.

Based on the initial observations from the thin sections, it is apparent that there is no wear of presumed older, more posterior cusps compared to the presumed younger, more anterior cusps. This conclusion is based on the continuous and uniform layer of orthodentine covering all of the teeth along the bony plate (Fig. 2.11).

As mentioned, from the CT-scan data, it appears that the teeth are very deeply inserted into the bony plates, and do not rest almost on the surface of the plates like those seen in the Tetanopsyridae (see above). The pulp cavity and the tooth crowns can be distinguished from the rest of the bony base of the dentigerous plate, exhibiting a different form of growth or tooth addition than what was proposed by Ørvig (1973).

Remarks—This study does give some insight into how the bony, dentigerous plates and their underlying cartilaginous jaws grew. The teeth increase in size anteriorly in the mouth and the cartilages usually extend more anteriorly than the dentigerous bony plates.

Gross (1971) suggested that the dentigerous bones of ischnacanthids may have been shed repeatedly during the life of the fish and were re-grown bearing larger teeth. Ørvig (1973), however suggested a continual addition of teeth to the anterior end of the dentigerous plate throughout ontogeny, as well as a wearing-down of the smaller, posterior, older teeth. There is no evidence for wear in the teeth from the ischnacanthids from the MOTH locality, and I have yet to see an area of growth where the dentigerous plate and associated tooth is being added.

It is doubtful that the entire bony plates were shed periodically thoughout the life of the animal as there would be some evidence of this in the fossil record. This would be seen as ischancanthids preserved with cartilaginous jaws and no overlying bony plates, or with an extra replacement set of bony plates ready to push out the older set. Although there have been ischnacanthids found without cartilages but with bony plates, the opposite has not been reported.

I am drawn to Ørvig's (1973) suggestion that the dentigerous plates grow throughout ontogeny, but instead of the teeth all being morphologically similar and worn down during life, it is more likely that the teeth changed morphologically throughout ontogeny to support a changing feeding style. The histological analysis done on these dentigerous bony plates suggests this as there is a continuous layer of orthodentine seen throughout the series of tooth crowns. From the histological analyses I am also able to conclude that there is a clear separation of the teeth from the base of the bony plates. This disagrees with the mode of growth proposed by Ørvig (1973), in which each tooth unit includes the entire height of the crown plus the underlying portion of the dentigerous bony plate.

Hermus (2003) suggested that the ischnacanthids retained a constant number of teeth throughout ontogeny and that the teeth grew in size accordingly with the fish. She also found no evidence for wear in the older teeth. I tend to disagree with these findings, as Hermus had a very small sample size and this type of growth has not been suggested in any other study of Ischnacanthiformes.

Valiukevičius (1992) noted that in *Poracanthodes menneri*, another ischnacanthid acanthodian, the largest teeth on the bony plates were in the middle of the plates and not in the anterior-most position. Hermus (2003) agreed somewhat, noting that the anterior-most tooth is generally much smaller than the second tooth. Is this an example of an intermediate growth form, showing the addition of the newer teeth? Comparative histological and morphological work between the jaws of *Poracanthodes* and *Ischnacanthus* must be done before any firm conclusions can be made.

DISCUSSION

As seen in this study, there is a great deal variation in the different morphologies of preserved jaws in the Eugnathostomata from the MOTH locality. There are differences between the preserved jaws of putative chondrichthyans and acanthodians, but also much variation within the Acanthodii. The presence and absence of teeth in these various forms of jaws should be noted and compared with other known representatives of the Eugnathostomata that were present in the Devonian.

The preserved jaws of the putative chondrichthyan *Kathemacanthus rosulentus* have a very grainy texture and have been concluded to have formed by calcification (probably globular) of the cartilage. In all of the acanthodians with preserved jaws in this study, the cartilages have been ossified and not calcified like those seen in the putative chondrichthyans. The texture of the acanthodian cartilages is not grainy like calcified cartilage, but smooth, resembling the endochondrally formed pectoral girdles. It is likely that the jaw cartilages were ossified in a similar manner.

From this, it is most likely that in all cases of putative chondrichthyans with preserved jaws the jaws will be calcified by some mechanism (either by globular [as in *Kathemacanthus rosulentus*; see above], or prismatic calcification [as seen in *Doliodus problematicus*; Miller et al., 2003]). It is also likely that all of the preserved cartilages in acanthodians have been endochondrally ossified.

Putative Chondrichthyan Jaws

As noted above, *Kathemacanthus rosulentus* is the only species of putative chondrichthyan from the MOTH locality with preserved, calcified jaws. Both the palatoquadrate and Meckel's cartilages are calcified, comprising the upper and lower jaws, but there are no associated bony plates or teeth. The long symphysis between the Meckel's cartilages most likely held the lower jaws at a certain angle to aid in feeding.

Although *K. rosulentus* is the only putative chondrichthyan with calcified cartilage jaws, it is not the only putative chondrichthyan from the MOTH locality. There are several putative chondrichthyans without calcified cartilages, but that did possess teeth and other dental structures (see Chapter 3). This may indicate that calcification of the cartilages is a functional morphologic trait to aid in certain modes of feeding, whereas the other putative chondrichthyans from this locality had teeth, and perhaps a different feeding style.

The jaws of *K. rosultentus* should be compared to those of the oldest articulated chondrichthyan, *Doliodus problematicus* (Miller et al., 2003). The cartilages of *D. problematicus* were also calcified and were supporting teeth. A comparison of the different morphologies of the calcified jaws in both of these species may give some insight into how and why these structures were preserved, and help clarify the relationships of *Kathemacanthus*.

Acanthodian Jaws

There is much variation in the morphology of the dentigerous 'jaw bones' found in the acanthodians from the MOTH locality. With the exception of *Gladiobranchus probaton*, they all have ossified palatoquadrate and Meckel's cartilages overlain by bony dermal plates. In the case of *G. probaton*, only the anterior part of the Meckel's cartilage is ossified.

There has been a great deal of information gathered by various researchers throughout the years, giving a more complete record of *Ischnacanthus* and its jaws. From this study it is clear that the cartilages and the dentigerous bony plates grew as the fish grew throughout ontogeny. It is very likely that the teeth were added in the anterior position and changed morphologically throughout ontogeny from a lower, more rounded, crushing tooth form, to a larger, more pointed tooth form. This type of change in tooth type throughout ontogeny is not uncommon in acanthodians, as is seen in their tooth whorls (see Chapter III).

It is also clear that the cartilages grew anteriorly beyond the bony plates, most likely to provide support for the symphyseal tooth whorls as well as to provide space for the growing tooth plates. It is still unclear exactly how the teeth were added to the tooth row, but it is evident from the histological data that the teeth are deeply inserted into the bony base and that there is a separation between the teeth and the rest of the bony base. It seems most likely that the base would grow before the new teeth were added, and this is similar to the condition seen in the acanthodian tooth whorls (see Chapter III).

In Ischnacanthidae and Tetanopsyridae, the ossified cartilages are overlain by bony plates, which usually are supporting one or more rows of teeth (the exception is *Tetanopsyrus breviacanthias*, which shows no evidence for teeth/denticulation). The commonality of the preserved jaws with dentigerous bony plates of these two groups suggests that they are closely related; it is doubtful that this type of structure would have evolved twice, independently.

This puts into question the evolutionary position of both *Tetanopsyrus breviacanthias* and *Gladiobrachus probaton*. Is *T. breviacanthias* an example of an intermediate form between ossified jaws alone and the ossified jaws with dentigerous bony plates, or is it a more derived form that secondarily lost the teeth on the bony plates? I feel it is more likely that it is the latter because the jaws and dentigerous plates of the ischnacanthids are well established and the other two representatives of the Tetanopsyridae both possess some form of dentition on their bony plates.

Does this then suggest that *Gladiobranchus probaton* is more or less derived than the Ischnacanthidae and the Tetanopsyridae? *Gladiobranchus* and the family Tetanopsyridae are both part of the Diplacanthiformes, making them more closely related to each other than either is to the Ischnacanthidae. However, the morphological similarities between the ossified jaw complexes of the Tetanopsyridae and the Ischnacanthidae are striking and put into question the evolutionary place of *Gladiobranchus* and even *Diplacanthus*, which has similar ossified Meckel's cartilages (Watson, 1937). Do these two forms show a reduction of cartilages and secondary loss of dentigerous bony plates, or are they primitive forms whose ancestors never had 'jaw bones'?

To answer any of the questions posed above, more histological thin-section work needs to be done to establish the exact composition of the dermal bony plates. This information can then be placed into a phylogeny, hopefully to give some resolution to this problem. From this study, it does seem likely that the Ischnacanthiformes and Diplacanthiformes are very closely related to each other, and possibly less closely related to the other forms of acanthodians.

Evolutionary Implications

One of the main questions to be asked is, are teeth needed to derive jaws or vice versa? According to Smith (2003), the evolution and development of teeth and jaws are separate and do not influence each other. This belief also supports the idea that teeth may have evolved more than once (Smith and Johanson, 2003; Johanson and Smith, 2003, 2005).

Johanson and Smith (2003, 2005) propose that the whorl-like arrangement of pharyngeal denticles in the thelodont *Loganellia* are homologous to the placoid scales and teeth seen in sharks, making teeth appear before and develop independently from jaws. This seems unlikely as there is no evidence for such homologous structures seen in the Osteostraci (a commonly considered sister group to the gnathostomes; Donogue and Sansom, 2002).

Within the Placodermi, the first jawed vertebrates (Janvier, 1996), Johanson and Smith (2003, 2005), and Young (2003) proposed that teeth are present. It is unlikely that these 'teeth' are homologous to those seen in the Eugnathostomata because they only develop in the very derived forms belonging to the Arthrodira.

In all of the early Eugnathostomata from MOTH discussed in this thesis and in Hanke (2001), jaws are present (or assumed to be). In some of the forms considered more primitive, such as the putative chondrichthyan *Obtusacanthus corroconis* (see Chapter 4, this thesis; Hanke and Wilson, 2004), and the acanthodian *Lupopsyrus pygmaeus* (Bernacsek and Dineley, 1977), the jaws are not preserved, and there are no teeth present. Teeth, calcified/ossified jaws, and dentigerous jaws do not appear until the more derived forms. This supports the theory that jaws evolved before teeth (Donoghue and Sansom, 2002).

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III. TOOTH WHORLS AND ASSOCIATED TEETH AND TOOTH-LIKE STRUCURES OF EUGNATHOSTOMATA FROM THE LOCHKOVIAN (EARLY DEVONIAN) MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA

INTRODUCTION

Origins of Teeth

The study of the origin of teeth is still a very wide open field, with little certain information. There are multiple contradicting theories as to how they evolved and developed (Johanson and Smith, 2005; Hertwig, 1874), which makes better understanding of how tooth whorls grow and change important whorls share similar features with the labial and rostral scales of some of the Ischnacanthidae (see Chapter IV). These similarities could imply some evolutionary links to the origin of teeth.

Comparisons between the tooth whorls seen in chondrichthyans and acanthodians have also been made to the whorl-like rows of denticles seen in the pharyngeal region of the thelodont *Loganellia scotia*, as well as to patterns of denticulations seen in some derived placoderms (Smith, 2003; Johanson and Smith, 2003, 2005). A better understanding of the histology and comparative morphologies of the tooth whorls of the various gnathostomes from the MOTH locality will hopefully suggest some resolution to this problem, or at least provide some clarification of the alternatives.

The currently best-accepted definition of a tooth is that of Reif (1982), the originator of the Odontode Regulation Theory of tooth formation (see Chapter I). Reif classified a tooth as an element of dentition formed by a dental lamina, which prefabricates replacement teeth before the current tooth is shed. A denticle is formed superficially at the epithelium-mesenchyme surface and does not originate in an invagination. Teeth are also organized into families and rows, whereas denticles are largely unorganized and do not necessarily have a pattern.

Tooth Whorls

Tooth whorls are often discussed in the literature but rarely in great detail. The best-known tooth whorls belong to the acanthodians *Ischnacanthus* and *Climatius* (Watson, 1937), the onychodontiform sarcopterygians *Onychodus* and *Strunius* (Andrews et al., 2006), and the Carboniferous sharks such as *Helicoprion* and *Edestus* (Hay, 1909). They are usually found in a symphyseal or parasymphyseal position in the oral cavity, but can also be found lining the upper and lower jaw margins. Relatively little is known about their comparative morphologies, histologies, and growth.

The term 'tooth whorl' is a very broad one and can be confusing when homologies among different groups are assumed. For example, sarcopterygian tooth whorls are very different from those seen in chondrichthyans, acanthodians, and putative chondrichthyans. In addition, tooth whorls and associated structures are more prevalent within the Acanthodii and Chondrichthyes than generally realized. These different types of whorls need to be examined more closely to understand better their histology and growth. This information can lead to better knowledge of ontogenetic change as well as improved ideas about evolutionary origins of the different kinds of teeth.

In both acanthodians and chondrichthyans, where tooth whorls are often found in situ, the whorls grow lingually to labially, with the youngest, largest tooth also being in the lingual-most position (Ørvig, 1973; Zangerl, 1981). The youngest tooth would be the next to take the functional position, rotating into place while the older tooths rotate out of the functional position. This is a similar growth pattern to what is seen in tooth families in extinct and extant sharks (Williams, 2001), except that in those cases multiple younger teeth can be developing, and the oldest of these rotates into position to replace the shed tooth. The increase in tooth size accommodates growth of the fish. For this study, I assume the same to be the case in the tooth whorls examined, whether or not they are found in situ.

Associated Tooth Types

Many taxa within the Eugnathostomata possessing tooth whorls also possess other, associated teeth or tooth-like structures, independent from the jaws (see Chapter II). These structures can include: pharyngeal denticles in sharks

(Nelson, 1970), a variety of isolated tooth-like elements in the pharyngeal and branchial regions of acanthodians (Pultschuppen in *Nostolepis striata*, Gross, 1971; tooth-like cones in branchial region of *Poracanthodes menneri*, Valiukevičius, 1992; 'gill rakers' in *Homalacanthus connicus*, Gagnier, 1996; as well as the various structures discussed below), and the multiple bony tooth-bearing plates in actinopterygians (e.g., *Cheirolepis canadensis*, Arratia and Cloutier, 1996) and sarcopterygians (e.g., *Onychodus jandemarrai*, Andrews et al., 2006).

Some derived placoderms also have an assortment of denticulations or so-called 'teeth' on the various dermal elements of the jaws and head that are considered by some to be an isolated dentition homologous at some level to teeth of other groups (e.g., Johanson and Smith, 2003, 2005; but see Young, 2003). However, it is unlikely that all of these associated 'teeth' are homologous with true teeth as defined by Reif (1982). The morphological descriptions and reinterpretations of the associated tooth types seen in the eugnathostomes from MOTH will hopefully clarify some of the homologies and phylogenetic relationships among these various species.

Tooth Whorls in the Eugnathostomata from the MOTH Locality

In this chapter, I will give detailed descriptions of the tooth whorls and associated teeth and tooth-like structures of the representatives of the Eugnathostomata (see Chapter I) from the Man on the Hill (MOTH) locality in the Northwest Territories, Canada. This fossil site has produced an abundance of tooth whorls belonging to both of these groups, found both isolated and associated with body fossils. These whorls are either complete or nearly so. These fishes show great diversity in tooth whorl morphology as well as in location in the mouth. In some cases, the whorls line the entire upper and lower jaws, and in others, they are restricted to the front or back part of the oral region.

Within the different taxa, I compare the morphology and histology of the associated tooth whorls to identify any similarities or differences in the structure and possible growth patterns of the teeth. I describe in situ, isolated, and extracted whorls, as well as similar elements of the associated dentition in and around the jaw margins.

Gross (1971) was one of the first and last researchers to attempt to understand better the morphology and histology of tooth whorls within the Eugnathostomata. The tooth whorls that were available to him at the time were few in number and lacking in preservation quality. The variety and exceptional preservation of the newly discovered tooth whorls from the MOTH locality will serve to extend his initial study.

Terminology and Methods

Because many of the elements studied are found isolated, it is not always clear if the tooth whorl being studied is from the upper or lower jaws or if it is from the right or left side of the jaws, or whether it was in a symphyseal or parasymphyseal position. Although some of the information about the tooth whorl is unknown when it is found isolated, there are some indicators of growth in the whorls, and some anatomical terminology should be clarified before going into detailed morphological descriptions of the different whorls.

The term medial refers to the middle or center line of the whorl, and the term lateral refers to one side of the whorl or the other. If there are multiple rows of teeth on a whorl, the central row is the medial tooth row and the side rows are the lateral tooth rows (Fig. 3.1A). If there are lateral cutting edges on some of the teeth, these edges are not pointing into or out of the mouth, but to the sides of the whorl (Fig. 3.1C).

As mentioned above, the tooth whorls grow lingually to labially, like tooth families of sharks (Williams, 2001). Lingual points to the inside of the mouth, toward the tongue if one was present, and is where the largest, youngest tooths are found; labial points to the outside of the mouth, in the direction of the lips if any, and this is where the oldest, smallest teeth are found (Fig. 3.1B, C).

When referring to the base of the tooth whorls, the thickness (Fig. 3.1C) of the base is measured in side profile of the whorl and the width of the base is measured in basal view (Fig. 3.1B).

For complete methods, locality and age information see Chapter I.

Institutional and Locality Abbreviations—**MOTH**, Man On The Hill locality, Northwest Territories, Canada; **NMC**, Canadian Museum of Nature,

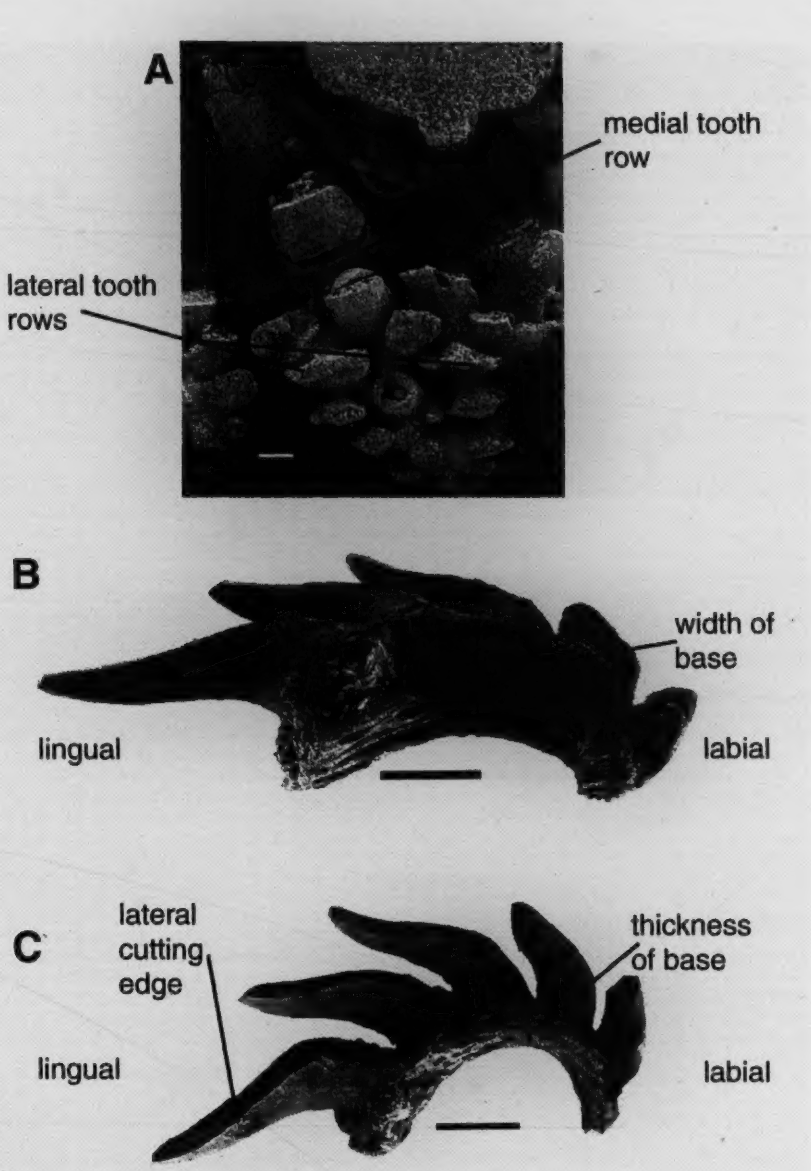

FIGURE 3.1. Clarification of anatomical terms. **A**, UALVP 41708, *Brochoadmones milesi* tooth whorl in crown view; **B**, UALVP 42525, tooth whorl of Gen. Nov. C et sp. nov. A in basal view; **C**, UALVP 42525, tooth whorl of gen. nov. C et sp. nov. D in side view. Scale bar for **A** equals 100um, all other scale bars equal 1mm.

formerly National Museum of Canada, Ottawa; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton.

Anatomical Abbreviations—**aa**, area of attachment; **az**, attachment zone; **b**, base of tooth; **bt**, basibranchial teeth; **dc**, denticulated cusp; **flp**, finger-like projection; **fp**, fusion point; **k**, keel; **lrtr**, lower right tooth row; **ls**, labial scales; **ltr**, lateral tooth row; **mc**, mandibular canal; **mk**, Meckel's cartilage; **mp**, mosaic plate; **mtr**, medial tooth row; **pbc**, piggy-back cusp; **pc**, pulp cavity; **pce**, primary cutting edge; **pd**, pharyngo-denticle; **pq**, palatoquadrate cartilage; **psp**, pointed stellate plate; **rp**, rosette plate; **rs**, rostral scales; **sb**, stellate branch; **sce**, secondary cutting edge; **sp.**, stellate plate; **str**, striation; **stw**, symphyseal tooth whorl; **tc**, tooth crown; **tw**, tooth whorl; **ultr**, upper left tooth row; **urtr**, upper right tooth row; **vc**, vascularized canal; **yc**, youngest tooth crown.

SYSTEMATIC PALEONTOLOGY

Superclass GNATHOSTOMATA

EUGNATHOSTOMATA DeIuliis and Pulera, 2007

Class CHONDRICHTHYES Huxley, 1880

Order incertae sedis

Family incertae sedis

Gen. Nov. B

Diagnosis—Diagnosis based on dentition; for additional diagnostic features, see Hanke (2001:158-159). Putative chondrichthyan with mouth, large, and terminal; head scales lacking; palatoquadrate and Meckel's cartilages unossified; tooth whorls present, lining upper and lower jaw margins; tooth whorls each with three rows of older, rounded teeth in battery, changing into single row of younger, pointed teeth fused to recurved base; tooth whorls grading into stellate plates extending into branchial region.

Gen. Nov. B et sp. nov. A

(Figs. 3.2-3.5)

Diagnosis—Diagnosis based on the dentition; tooth whorls large, robust; whorls largest at the symphysis, decreasing in size posteriorly along jaw margin; oldest teeth small, rounded; teeth before transformation to single row raised, rectangular and forming battery; all teeth in multiple rows tightly packed; teeth in single row large, pointed, directed into oral cavity; tooth whorls grading into stellate plates lining inside of oral cavity; stellate plates made up of nine to twelve radiating branches, giving snowflake-like appearance; specialized, pointed, tooth-like stellate plates in floor and roof of oral cavity; rosette-like plates in lower jaw, grading into mosaic plates, grading into stellate plates.

Material—UALVP 43408, 44044, 41993. For additional specimens, see Hanke (2001).

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—Gen. Nov. B et sp. nov. A is a putative chondrichthyan that was first described by Hanke (2001:158-183). A more detailed, formal description is in preparation by myself and Hanke. There are two articulated specimens, UALVP 43408 and 44044, which show the whorls and stellate plates in situ. Although UALVP 43408 is better for preservation of overall morphological detail of this species, UALVP 44044 is larger and shows more detail of the oral region, including whorls, stellate plates and the gape of the mouth, and will be used for most of the in-situ descriptions of these structures. Recently, a new, partially articulated specimen of this species has been discovered, UALVP 41993. This specimen is important because it shows the best preservation of the tooth whorls, allowing for a much more detailed description and understanding of the differences between this species and the related Gen. Nov. B et sp. nov B. Unfortunately, because this specimen was just recently discovered, histological work such as thin-sectioning or CT scanning was not possible.

UALVP 43408 is a putative chondrichthyan of medium body size that has been preserved with the head dorsoventrally compressed and the body laterally compressed (Fig. 3.2A). This specimen does not show the morphology of the tooth whorls or stellate plates in crown view, but does show it in basal view. The

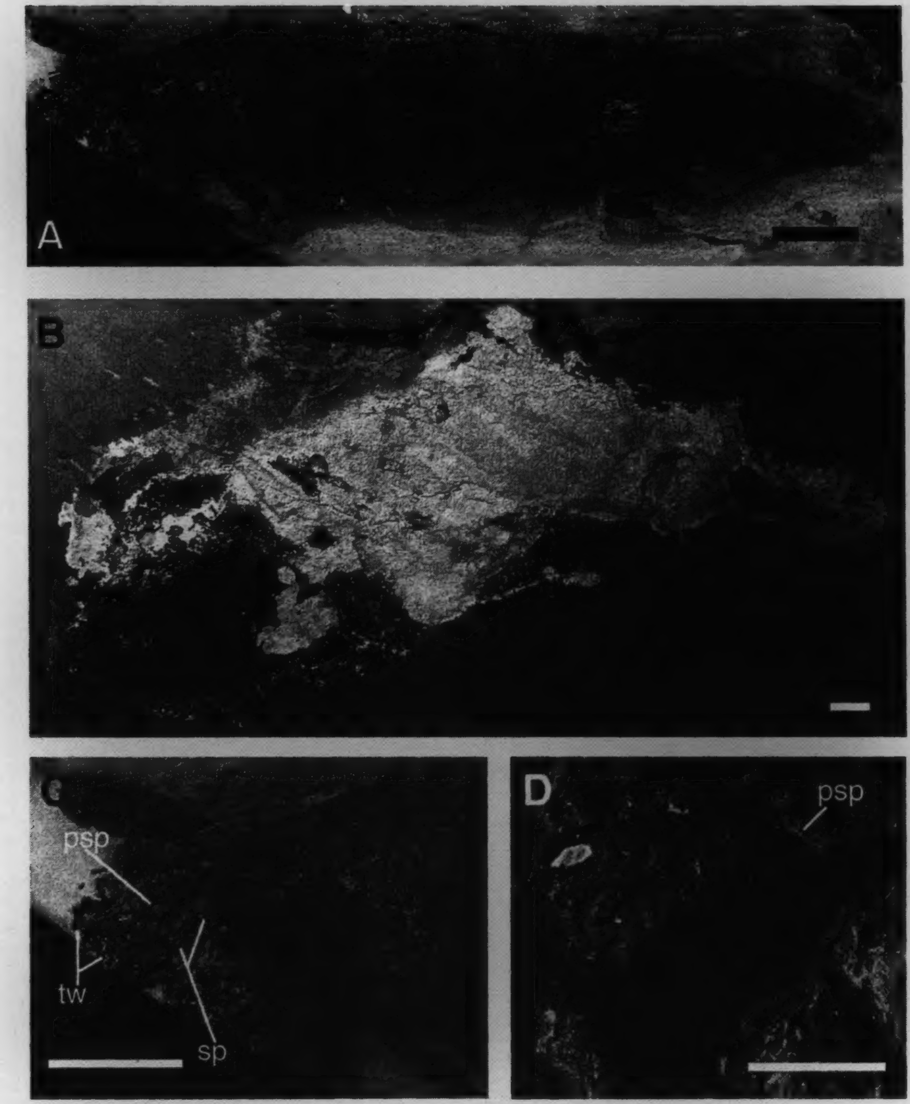

FIGURE 3.2. Gen. Nov. B et sp. nov. A. **A**, UALVP 43408 (holotype) whole body in dorso-side view; **B**, UALVP 44044 whole body in side view; **C**, close-up view of the head of UALVP 43408, with tooth whorls and stellate plates in basal view; **D**, close-up view of the pointed stellate plate of UALVP 44044. Scale bars equal 1cm.

bases of the tooth whorls and stellate plates are concave and vary in size and shape (Fig. 3.2C). The bases of the whorls are more curved and have canals along the bottom of the base as well as through the whorl; the bases of the plates are only slightly concave and have only canals going into the base and crown. The intermediate forms of these two structures are conical at the base and also just contain only canals going into the base.

The only other articulated specimen (UALVP 44044) shows the tooth whorls and stellate plates in both basal and partial crown view (Fig. 3.2B). The head is compressed laterally and the gape of the mouth is visible, as are areas in the oral cavity that give information on position/location of the whorls and stellate plates. In this specimen, the whorls line the anterior half of the jaw margin. They are more scattered at the anterior-most part of the gape, and are larger in size. Most of the whorls have been preserved in basal view, but there are at least 9 tooth whorls that can be seen in side or crown view. The palatoquadrate and Meckel's cartilages are unossified, and it is unclear which of the whorls belong to the upper and which to the lower jaws (Fig. 3.3).

Tooth Crowns—The tooth crowns are arranged in three rows to form a battery of teeth. The crowns of the teeth in the medial row are low and rounded, with a somewhat flat top that becomes more rounded as the teeth become larger. There are generally seven to nine teeth in this row (Fig. 3.5).

In the lateral rows, the teeth line up with those in the medial row. These teeth are long and rectangular, and have a flat, oval crown. None of the teeth in

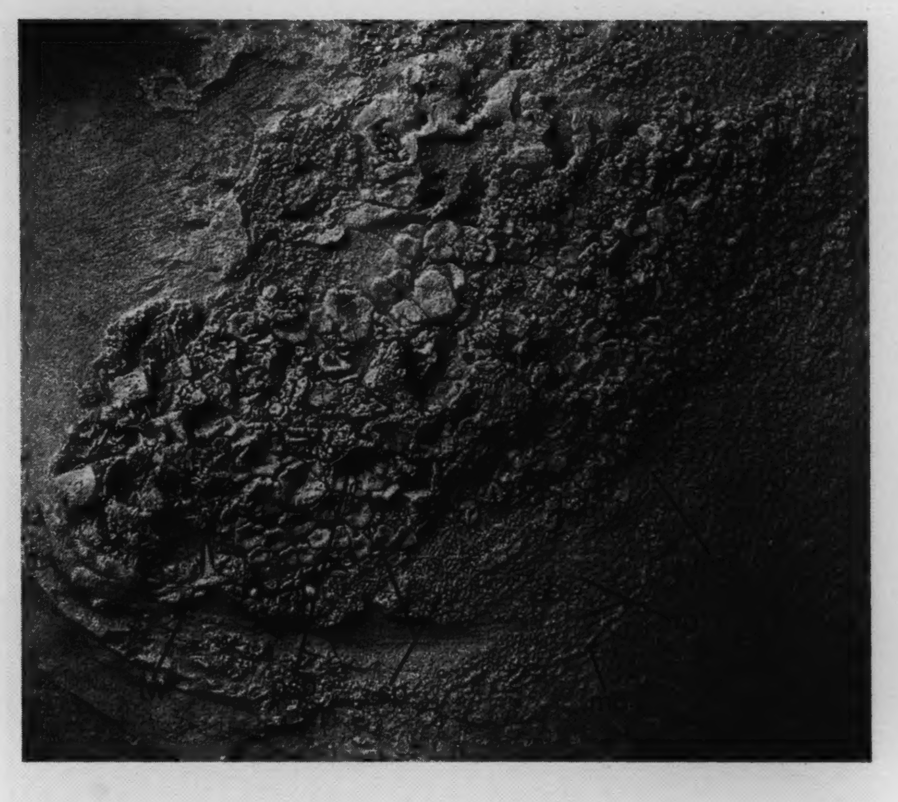

FIGURE 3.3 . Gen. Nov. B et sp. nov. A, head of UALVP 44044, highlighting dentition and the specialized tooth types. Scale bar equals 0.5cm.

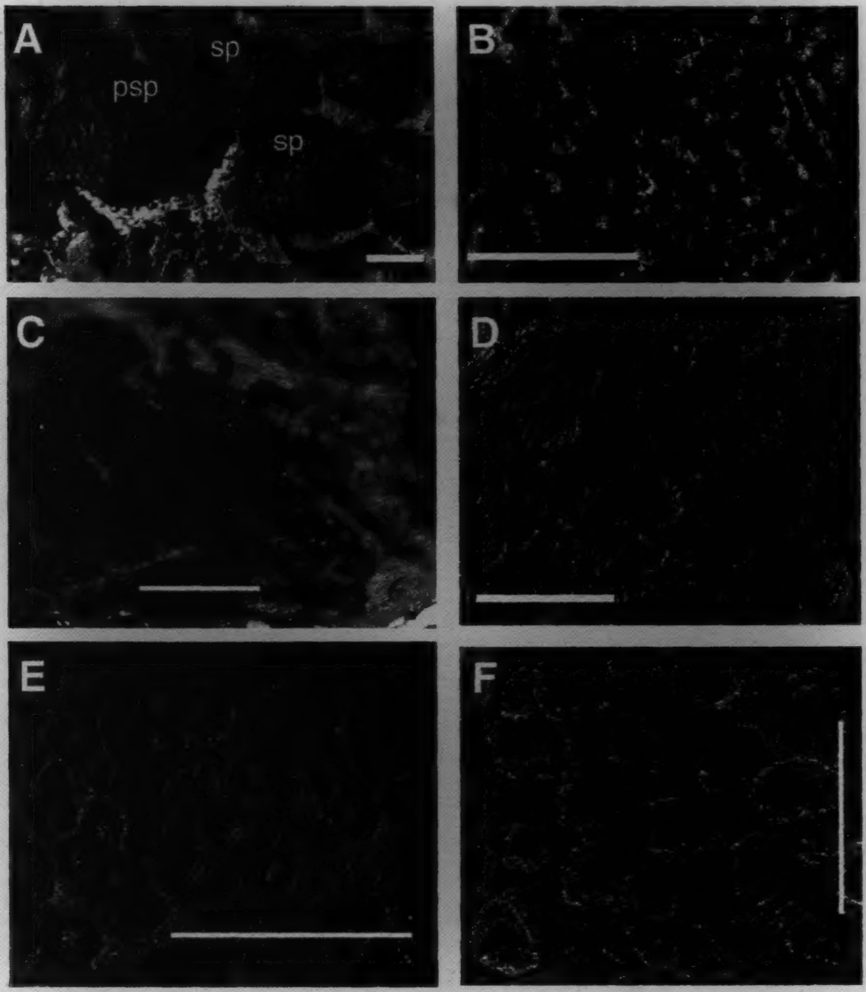

FIGURE 3.4. Gen. Nov. B et sp. nov. A, UALVP 44044, close up views of specialized dentitions. **A**, stellate plates and pointed stellate plates in basal view; **B**, stellate plates in crown view; **C**, pointed stellate plate in crown view; **D**, mosaic plates (scale bar equals 0.5mm); **E**, rosette plates in basal view; **F**, rosette plates in crown view. Scale bars equal 1mm.

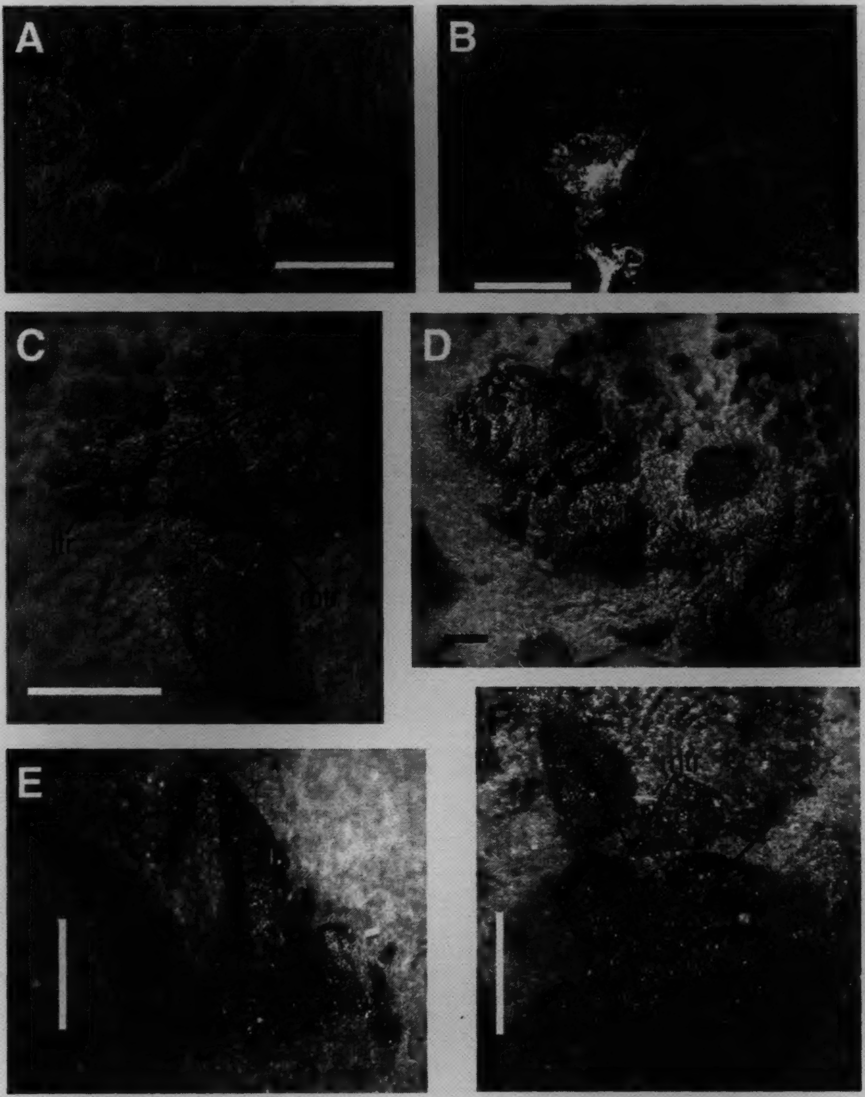

FIGURE 3.5. Gen. Nov. B et sp. nov. A., **A-B**, UALVP 44044, **C-F**, UALVP 41993. **A**, youngest tooth in a tooth whorl; **B**, tooth whorl seen in side view, lingual is left; **C**, tooth whorl seen in crown view, lingual is down; **D**, various tooth whorls seen in crown view, note the three rows of teeth forming a battery; **E**, two large teeth of a tooth whorl, lingual is left; **F**, tooth whorl seen in crown view, ligual is to the upper left. Scale bars equal 1mm.

any of the rows shows any small-scale denticulation or ornamentation. All of the rows are tightly packed together (laterally and medially) and line up to form a type of battery (Fig 3.5D).

At a certain point, the morphology of the crown of the medial row of teeth changes from flat and rounded, to pointed and conical. When this change in morphology occurs, only the medial row persists and the lateral ones stop. There are two to three of these larger, conical teeth on each tooth whorl.

These conical teeth are slightly recurved, pointing in the lingual direction. On the sides of the larger teeth, there are cutting edges. The recurved edges wrap around the tip of the teeth from the lingual to the labial side; they are slightly more recurved than the teeth themselves (Fig. 3.5C, E, F). It is difficult to tell how far down on these teeth the cutting edges extend, as well as whether there are any secondary cutting edges. For future study, some of the tooth whorls on UALVP 41993 should be removed, further prepared and scanned with the SEM in order to see small-scale detail that may be defining of the tooth whorls of this species.

Bases of Tooth Whorls—In side view, the bases of the tooth whorls thicken only slightly as the larger, younger teeth are added. The bases are recurved, with the smaller, older teeth on the more tightly curved end (Fig. 3.5B). The amount of recurvature varies according to the position of the tooth whorls in the oral cavity and the size and age of the tooth whorl. The larger tooth whorls, found near the symphysis, have more recurvature (Fig. 3.3). The larger tooth whorls in UALVP 41993 have more teeth and a larger, more recurved base than the tooth whorls in UALVP 44044.

In basal view, the bases of the tooth whorls widen slightly to accommodate the larger, younger teeth. They are rectangular to triangular in shape. There are vascular canals extending into the bases in the side and the underside of the base. The canals are more numerous under the larger, younger teeth and are hardly evident on the older part of the tooth whorl (Fig. 3.3).

Internal Structure—No histological work (thin sections, CT-scans) has been done with the dentition of this species because the teeth in UALVP 44044 are too important to remove, being in-situ in the fish, and UALVP 41993 was just recently discovered and I have not had enough time to remove and sample them.

Due to the similarity in morphology of the tooth whorls and the stellate plates of this species to those seen in gen. Nov. B et sp. nov. B, it is fair to assume that they have similar histological structures. From the morphological data, it is evident that there are vascular canals extending into and through the base of the tooth whorl and I believe that they would extend, at least a little bit, into the teeth.

For further study, it would be useful remove and scan with the SEM various elements of the dentition (teeth, stellate plates, small rosette plates) from UALVP 41993. This would give a better and more complete histological picture of the dentition.

Attachment of the Teeth—As mentioned above, the tooth whorls grow by the addition of new teeth to the base at the lingual side of the whorl. From looking at the in-situ tooth whorls, it is unclear how the teeth were attached to the base. I would assume that the attachment of the teeth in this species would be similar to that seen in the other species of putative chondrichthyans discussed in this chapter. For a better understanding of the attachment, some of the tooth whorls should be extracted and analyzed with the SEM. The previously discussed histological work may also improve the understanding of the attachment of the teeth of the tooth whorl to their base.

In addition to changing size along the jaw margins, the whorls also appear to transform into stellate plates that cover the roof and floor of the mouth, extending into the branchial region (Fig. 3.2, Fig. 3.3). The tooth whorls are lining the anterior-most two-thirds of the upper and lower jaw margins and transform quickly into stellate plates covering the roof and base of the oral cavity.

Crowns of Stellate Plates—The stellate plates are best seen in situ in UALVP 44044. In crown view, these plates are stellate in appearance and are closely packed together; there is no clear differentiation between where one plate ends and the next begins. The largest plates appear to be from the middle of the floor and roof of the mouth and the smaller ones extend into the branchial region (Fig. 3.3).

The crowns of the plates are all morphologically similar, but not identical. The stellate pattern consists of radiating branches extending equally from a central point. Each branch has three to five small, paired projections extending from it, giving the plates a snowflake-like appearance. The number of branches is not consistent, but generally varies between five to nine, depending on the size of the plate (Fig. 3.4B).

Bases of Stellate Plates—The bases of the plates are flat to slightly concave. The plates have a geometrical shape, usually hexagonal, best seen in basal view.

In basal view, the fusion point of the plates is clearer and suture lines between the plates can be seen. The stellate plates also possess vascular canals, in the form of pores in the base extending into the crown of the plate as opposed to along the base, as was seen in the tooth whorls (Fig. 3.4A).

Conical Stellate Plates—There are also specialized, tooth-like stellate plates that still have a stellate crown, but are conical and much larger than the surrounding plates (Fig. 3.4C). There are two to three in both the upper and lower position in the oral cavity. A more detailed morphology of these specialized plates is not available as they are only found in the two articulated specimens and are partially covered in crown view by other stellate plates in basal view (Fig. 3.2C, Fig. 3.3).

In basal view, these specialized plates are very conical and vary slightly in size. Like the typical stellate plates, these plates also only have vascular canals that appear pore-like and extend into the crown (Fig. 3.2D, Fig 3.4A).

Rosette Plates—Rosette-shaped plates are found in the area of the lower jaw above the mandibular canals, extending back into the oral cavity (Fig. 3.3). They are small and closely packed together. These plates have been found in

UALVP 44044 in both basal and crown view and in UALVP 41993 in basal view. I am certain that the plates are internal as some of the plates seen in basal view overlap those in crown view, indicating they are inside the oral cavity.

The crowns of the rosette plates are made up of two to three rings that are slightly raised from the base. The rings are not perfect circles and have crimped ridges. The plates are slightly funnel-shaped, with the smallest ring in the center. The crowns of adjacent plates appear somewhat fused together, and it is not evident in this view where each plate begins and ends (Fig. 3.4F).

In basal view, they are dish-shaped. In UALVP 44044, they are found in this view in the most anterior part of the lower jaw, extending down to the mandibular canals (Fig. 3.4E).

Mosaic Plates—The mosaic plates are very small and tightly packed together. They are located behind the gape of the mouth in the pharyngeal region. The plates are preserved facing upwards and are slightly overlapping. They are fan-shaped with the rounded end facing ventrally, and the ridged, tapered end facing dorsally. They look somewhat like the body scales in their morphology, but they are much smaller in size and much thicker (Fig. 3.4D).

It is unclear if these plates are seen in basal or crown view. They extend from behind the rosette plates and are covered by the stellate plates in the pharynx (Fig. 3.3).

Remarks—I am confident that the stellate plates described above are in the oral cavity as opposed to being elaborate head scales. In both UALVP 43408 and 44044, these plates are seen in basal view, and there is nothing covering them. There is evidence that they are in the oral cavity by looking at UALVP 44044, focusing on the oral region. In this specimen, we can see that on the upper jaw, the plates are in basal view, and looking into the gape of the mouth, we see these plates in crown view. They overlap in places, crowns facing crowns, and this gives me confidence that they are in fact facing into the oral cavity, or into the branchial region.

The tooth whorls in this species are very organized, growing lingually to labially, and lining the upper and lower jaw margins. The stellate plates do not appear to have a pattern or organized mode of growth, but rather appear to grow until they come into contact with one another and partially fuse. The mosaic and rosette plates, although in the oral cavity and a part of the dentition, are much more scale-like in appearance and organization than tooth-like.

Gen. Nov. B et sp. nov B

(Fig. 3.6-Fig. 3.12)

Diagnosis—Putative chondrichthyan based on isolated, associated tooth whorls and stellate plates; oldest teeth in lateral rows with artichoke-like ornamentation; isolated stellate plates of varying size, shape, with five to nine radiating branches giving sun-like appearance.

Material—Isolated whorls: UALVP 42277.30, 42277.31, 42277.32, 42277.33, 42277.34, 42277.35, 42277.36, 42277.37, 42277.38, 42277.39.

Isolated plates: UALVP 42277.13, 42277.14, 42277.15, 42277.16, 42277.17, 4227718, 42277.19, 42277.20, 42277.21, 42277.22, 42277.23, 42277.24, 42277.25.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—UALVP 42277 is a block with associated but isolated tooth whorls and stellate plates believed to have belonged to a single specimen. From this block, fourteen partial or whole tooth whorls were removed (UALVP 42277.26-42277.39). This block is the only specimen of this species, but the remains are morphologically similar to those of Gen. Nov. B et sp. nov. A, placing them together in the same, new genus.

Tooth Crowns—The oldest teeth, arranged in three rows, are small, smooth and rounded, and have no detailed ornamentation (Fig. 3.6, Fig 3.8D). These teeth are found on the recurved, labial-most side of the base. There are usually four to six of these teeth in each row and they increase in size to accommodate the growth of the fish. The morphology of these teeth does not differ markedly between the medial and lateral rows.

The youngest one to two teeth in the lateral rows are larger and longer than the older ones, but are still rounded. These teeth are ornamented with two rings of pointed denticles, the lower row having larger denticles than the upper one. The denticles are pointed and face up, giving the teeth an artichoke-like

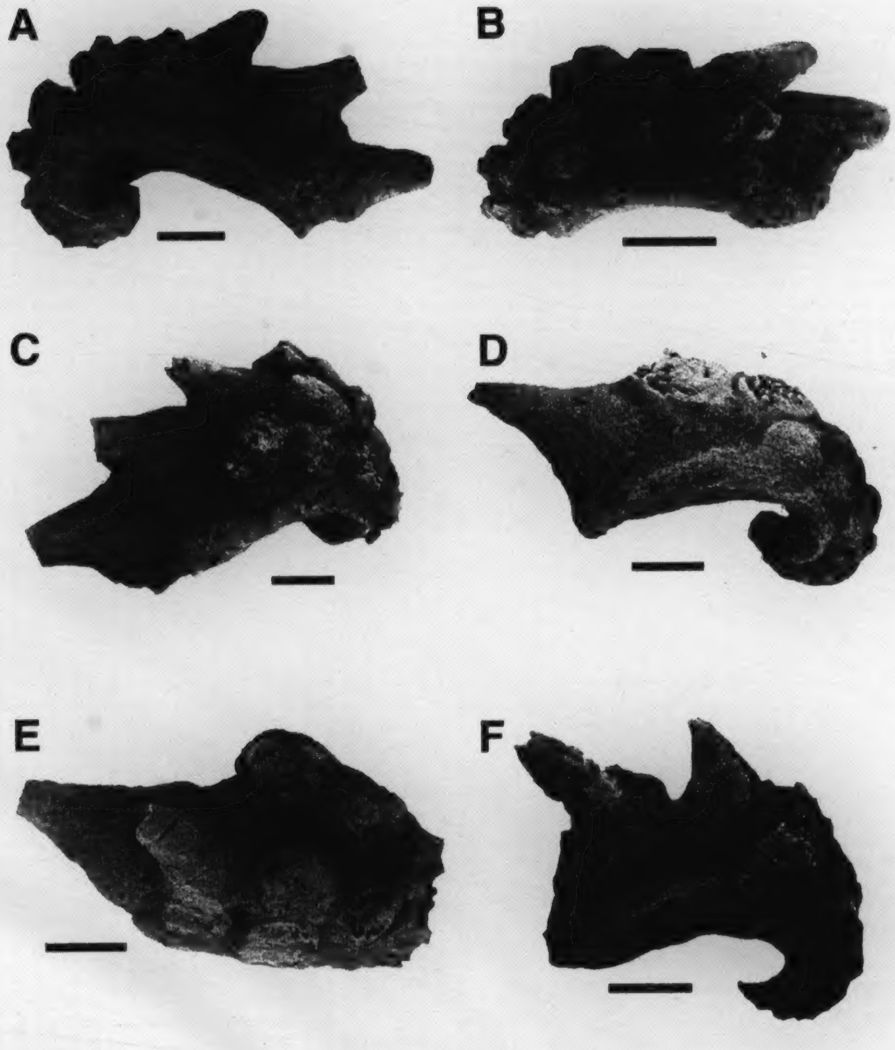

FIGURE 3.6. Gen. Nov. B et sp. nov. B, SEM images of assorted isolated tooth whorls, taken from the block UALVP 42277. **A**, UALVP 42277.29 from left side; **B**, UALVP 42277.31 from left side; **C**, UALVP 42277.34 from oblique right side; **D**, UALVP 42277.36 from right side; **E**, UALVP 42277.37 in crown view; **F**. UALVP 42277.38 from right side. Scale bars equal 1mm.

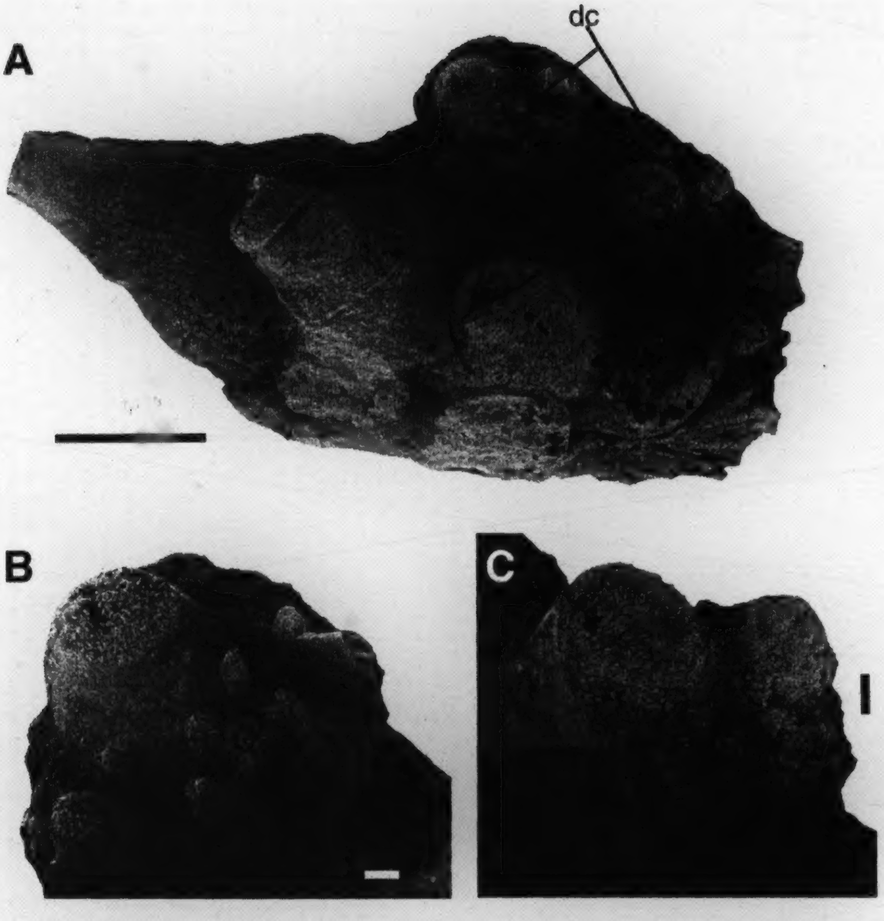

FIGURE 3.7. Gen. Nov. B et sp. nov. B, UALVP 42277.37 in crown view. **A**, intact tooth whorl showing undamaged, "artichoke"-like tooth crowns, scale bar equals 1cm; **B**, close-up of undamaged crown showing good denticulation; **C**, close-up of another denticulated crown. Scale bars for **B** and **C** equal 100um.

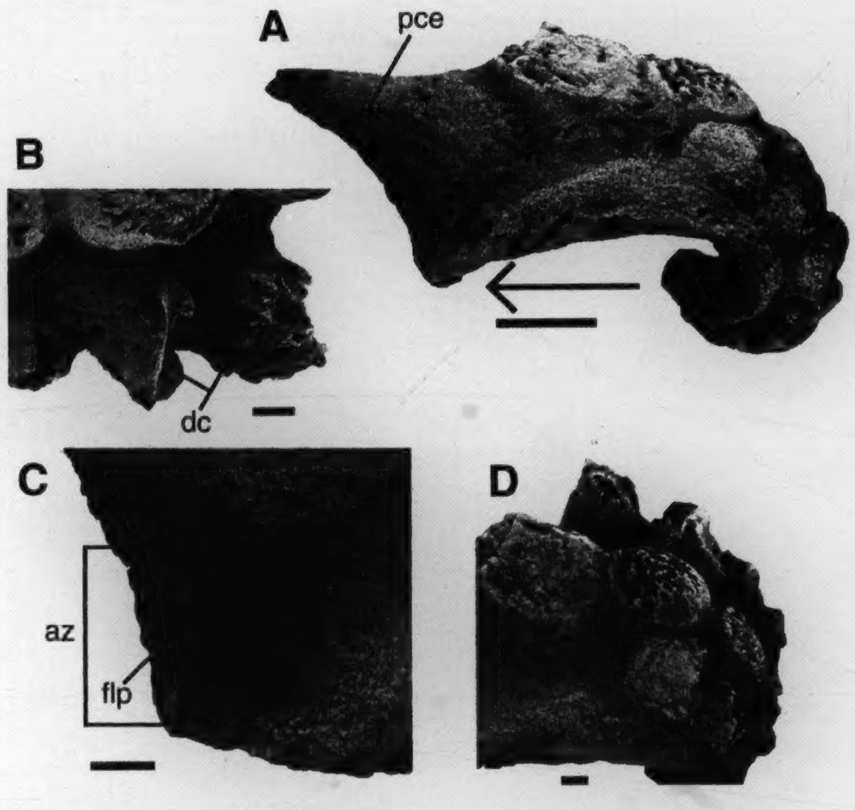

FIGURE 3.8. Gen. Nov. B et sp. nov B, SEM images of UALVP 42277.36. **A**, tooth whorl in side view, arrow shows increased width and thickness of base, lingual is to the left, scale bar equals 1cm; **B**, close-up view of the lateral, denticulated teeth; **C**, close-up of the attachment area of the youngest tooth; **D**, older teeth on the whorl, the attachment areas are much more fused to the base than the younger teeth. Scale bars for **B**, **C** and **D** equal 300um.

appearance (Fig 3.7). The ornamentation is preserved in different degrees of detail in the various whorls (Fig. 3.6), but this variation is probably an artifact of preservation or preparation. It is likely that all of the whorls had these ornamented teeth at a similar stage of development.

The youngest one to two teeth in the medial row do not share the same morphology as those in the lateral rows. These teeth are slightly longer and larger than the older teeth in the row, and they begin to point lingually (Fig. 3.6).

As the whorl grows and adds teeth, only the center row persists and the morphology of the teeth changes from small and rounded, to long and pointed (Fig. 3.6). The teeth gradually become more pointed than rounded in their crown and slightly curve in the lingual direction. On the lateral sides of the teeth, there are primary cutting edges that are slightly S-shaped (Fig. 3.8A). At the bottom of the primary cutting edge, there are one to three secondary cutting edges that extend ~40° posteriorly. Generally, there are two to three of these long, pointed teeth beyond the last teeth of the lateral rows. The teeth continue to increase in size with the newest/youngest tooth being the largest.

Bases of Tooth Whorls—The base of each tooth whorl is tightly recurved on the lingual end. The base increases in width as new teeth are added, accommodating the increased size of the teeth. Along with increasing in width, the base of the whorl also increases in thickness (Fig. 3.4).

In basal view, the recurved base has canals running along the base and through the whorl. It is believed that these canals were vascular canals used to supply blood and nerves to the whorl and individual teeth. The exact course of these vascular canals is evident from the CT-scan data and histological sections.

Internal Structure of Tooth Whorls—The vascular canals that can be seen extending into the base of the whorl also extend into the teeth of the whorl via smaller canals; this is evident from both broken teeth (Fig. 3.10A) and from CT-scan data (Fig. 3.9B). The teeth do not have a single pulp cavity, like many modern sharks (Zangerl, 1981), but have a network of canals throughout them that extend from the larger vascular canals running though the base of the whorl (Fig. 3.9B, Fig 3.10B).

This structure is also seen in a broken, isolated tooth, UALVP 42277.39. Because the tooth has been broken off, the internal structures can be clearly seen. There is not a single pulp cavity, but a series of networked canals (Fig. 3.10C, D).

Attachment of Teeth—Each new tooth becomes gradually attached to its base, and the zone of attachment is much clearer in the younger teeth than in the older ones (Fig. 3.8C, D). The teeth are attached by finger-like projections extending from the bottom of the tooth to the next youngest tooth, in a piggy-back fashion (Fig. 3.9), and then to the base of the whorl, the base appearing to grow as the tooth is being added.

In one specimen, UALVP 42277.38, the youngest tooth was only loosely attached and fell off during preparation (Fig. 3.11). From this, the process of attachment of the tooth to the base of the tooth whorl is better understood. On the lingual-most side of the base of the whorl, it is clear that the tooth was only

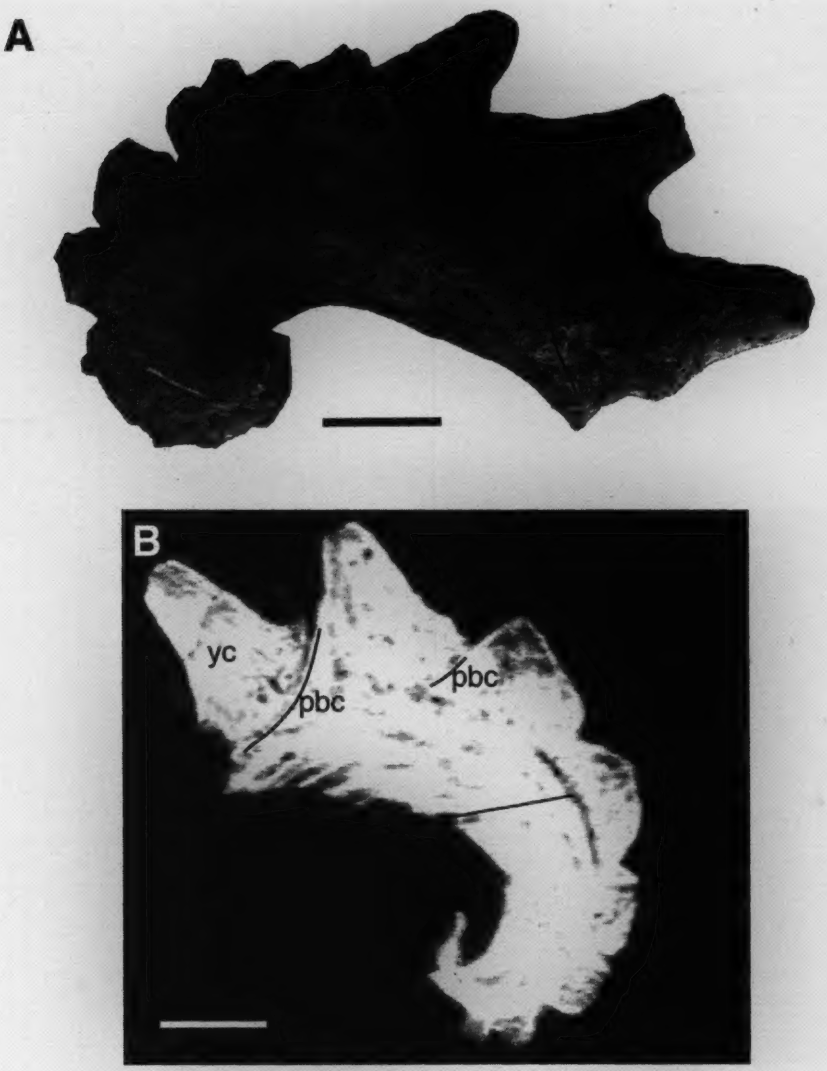

FIGURE 3.9. Gen. Nov. B et sp. nov. B, UALVP 42277.29. **A**, SEM image, with black lines added to show piggy-back attachment of the teeth; **B**, medial CT slice (099), the vascular canals in the base and teeth, the attachment area of the youngest tooth and the piggy-backed teeth are all clearly seen. Scale bar estimated at 1mm.

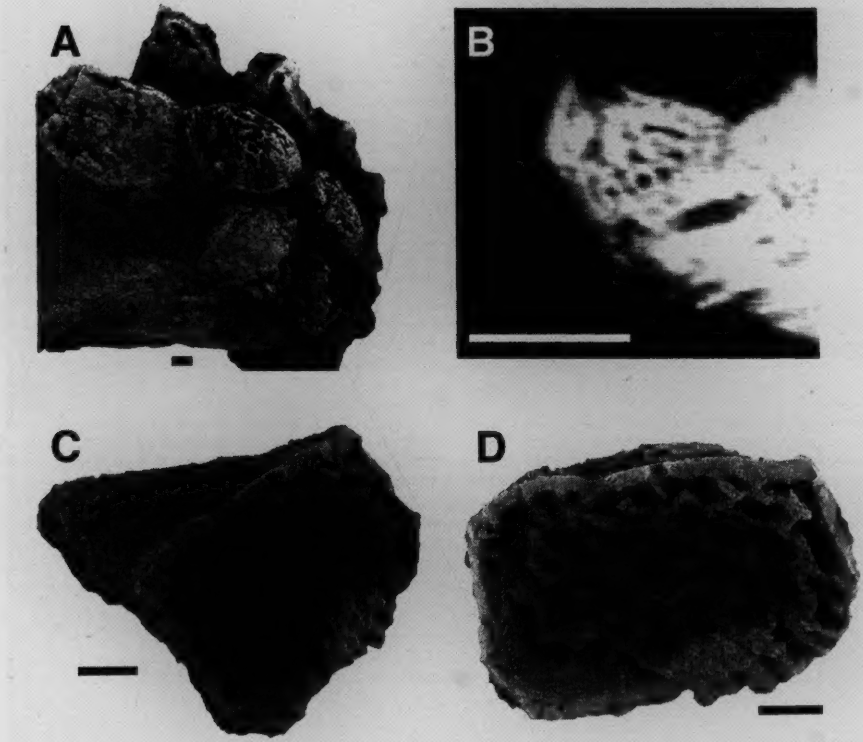

FIGURE 3.10. Gen. Nov. B et sp. nov. B, views of internal structure of teeth. **A**, UALVP 42277.36, broken teeth showing internal, vascularized canals; **B**, CT-scan (reslices 068) of youngest tooth of UALVP 42277.29 showing system of vsacular canals (scale bar estimated); **C,D**, broken, isolated tooth,UALVP 42277.39, in side (**C**) and basal (**D**) views. Scale bar for **B** equals 1mm, all other scale bars equal 200um.

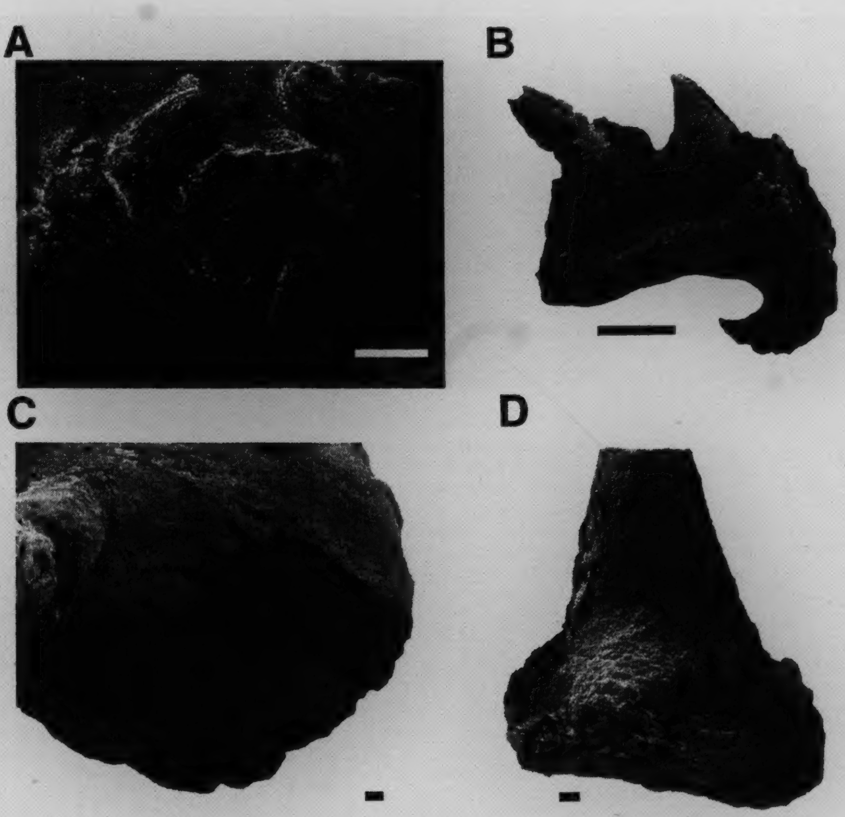

FIGURE 3.11. Gen. Nov. B et sp. nov. B, UALVP 42277.38. **A**, The tooth whorl before removal, the youngest tooth has not fully attached to the whorl; **B**, SEM image of the whorl after removal and preparation; **C**, lingual side of the whorl, the shading denotes the area where the tooth had not yet attached to the base; **D**, SEM image of the broken tooth, note the curve of the bottom of the tooth to piggyback onto the previous tooth. Scale bars for **A** and **B** equal 1cm, scale bars for **C** and **D** equal 100um.

attached to a third of its total attachment area. Interestingly, the vascular canals were already present throughout the entire base of the tooth crown as well as the area of attachment of the whorl (Fig. 3.11C, D).

Crowns of Stellate Plates—The stellate plates were found scattered on the same block on which the isolated tooth whorls were found. These plates are similar to those seen in Gen. Nov. B et sp. nov. A, but do show distinct morphological differences. Instead of a snowflake-like pattern, the stellate plates of Gen. Nov. B et sp. nov. B have radiating branches giving the appearance of a sun.

The crowns of the stellate plates consist of raised, radiating branches on a solid base. The branches zigzag slightly as they radiate from the center. The center, where all the branches meet, is not a single point, as it is in Gen. Nov. B et sp. nov. A, but a circle. The branches thus do not touch at their origin but radiate out from separate points on the circumference of the central circle (Fig 3.12A, C, D, E).

Bases of Stellate Plates—The bases of the stellate plates are very similar in morphology to those of Gen. Nov. B et sp. nov. A. They are slightly concave, have similar geometrical shape, usually hexagonal, and have vascular canals that extend into the crowns. The fusion lines of the plates are visible in basal view, and the edges fit in a mosaic pattern (Fig. 3.12B, F).

Remarks—Because the specimens of this species are isolated and from a single block, very little can be said about the variation in tooth whorl size and

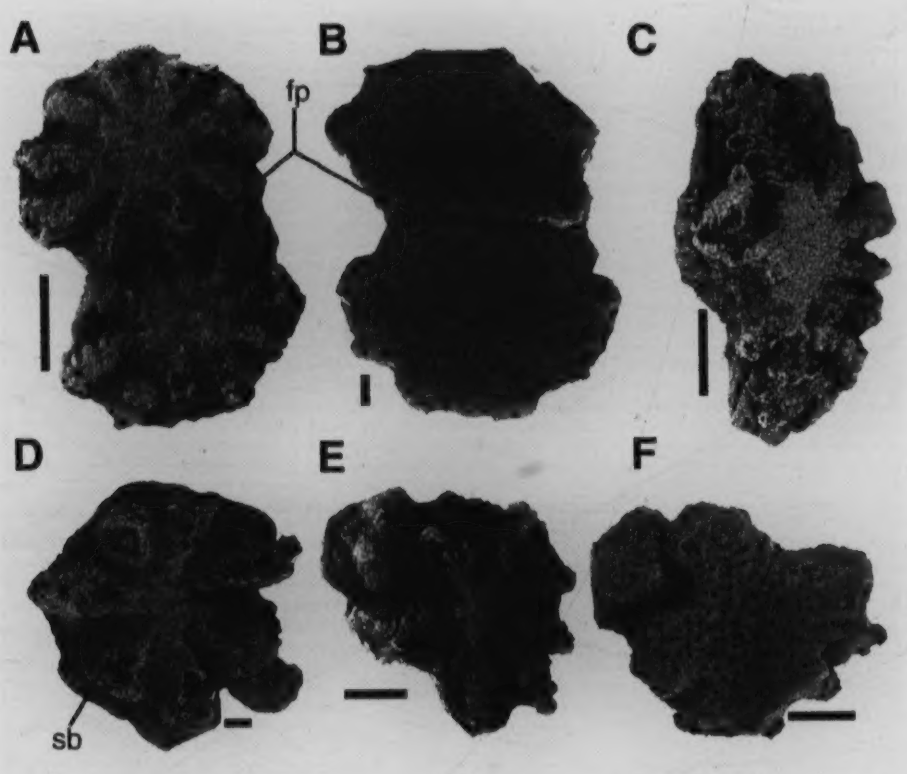

FIGURE 3.12. Gen. Nov. B et sp. nov. B, SEM images of isolated stellate plates from UALVP 42277. **A**, UALVP 42277.13, two fused stellate plates in crown view; **B**, UALVP 42277.13, two fused stellate plates in basal view, showing suture line between the two plates and the vascular pores; **C**, UALVP 42277.17, elongated stellate plate in crown view; **D**, UALVP 42277.15, stellate plate in crown view; **E**, UALVP 42277.14, a stellate plate with a smaller fused plate in crown view; **D**, UALVP 42277.14, a stellate plate with a smaller fused plate in basal view. Scale bars for **B** and **D** equal 300um, all other scale bars equal 1mm.

shape within the oral cavity. The same is true about the stellate plates; I cannot determine how they varied within the mouth in morphology and size. Due to the similarity in both the tooth whorls and stellate plates of this species to those of Gen. Nov. B et sp. nov. A, I believe that they would have similar size variation and positions in the oral cavity.

Although at first glance they are morphologically similar, I am confident that Gen. Nov. B et sp. nov. A and Gen. Nov. B et sp. nov. B are different species. Upon close inspection of the tooth whorls and stellate plates, many differences can be seen. The tooth whorls grow the same way ontogenetically, but in Gen. Nov. B et sp. nov. A, the older teeth are rectangular and closely packed like a battery. In Gen. Nov. B et sp. nov. B, the older teeth are more rounded and have an artichoke-like ornamentation. The stellate plates are also morphologically different. The stellate branches of Gen. Nov. B et sp. nov. A are thin and radiate out from a point (snowflake-like) whereas the branches of Gen. Nov. B et sp. nov. B are thicker and radiate out from a central circle (sun-like appearance). As well as these differences, a study comparing the body scales is ongoing and will hopefully provide even more proof that these two taxa are different species.

The stellate plates seen in the two species of Gen. Nov. B, in basal view, look very similar to the mucous membrane denticles seen in the articulated chondrichthyan *Doliodus problematicus* (see Figure 2 in Miller et al., 2003). In *D. problematicus*, these denticles are lining the mouth, similar to what is seen in the stellate plates of Gen. Nov. B. Could these be homologous structures, and these mucous membrane denticles seen in basal view? In the future, it may be beneficial to compare the stellate plates to these denticles and look for morphological similarities.

Gen. Nov. C

Diagnosis—Diagnosis of this putative chondrichthyan genus is based on isolated tooth whorls; no scales or other body parts have been found. Tooth whorl with base recurved; single row of pointed teeth, size increasing, lingually fused to base; teeth pointed, directed lingually; primary and secondary cutting edges on lateral sides of teeth; base size increasing with larger teeth; vascularized canals extending through base; piggy-back attachment of teeth; teeth lacking single pulp cavity, with system of vascular canals.

Gen. Nov. C et sp. nov. A

(Fig. 3.13-3.15)

Diagnosis—Putative chondrichthyan based on tooth whorl, with base slightly recurved, bearing 5 teeth; teeth pointed, fused to base, increasing in size lingually; larger teeth S-shaped, directed lingually; cutting edge more recurved than tooth; secondary cutting edges coming off lingual side of primary cutting edge; teeth striated above cutting edge; base thickening with addition of larger teeth; tooth attachment loose, by finger-like projections; teeth with piggy-back attachment; vascular canals extending through base of whorl and bottom of teeth.

Material—UALVP 42525.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—The holotype of Gen. Nov. C et sp. nov. A (UALVP 42525) is an isolated, putative chondrichthyan tooth whorl; it was found on a block without any associated body material. This tooth whorl has a slightly recurved base with five teeth. There is only one row of teeth and they get larger and become more recurved moving labially to lingually (Fig. 3.13).

Tooth Crowns—The labial-most tooth is small and blunt, and is firmly attached to the base. The tip of the tooth is broken, and the cutting edges are faint. There are no secondary cutting edges. The tooth is slightly curved, pointing lingually (Fig. 3.14D).

The next tooth has more of a point, but is still blunt. This tooth is also slightly recurved, pointing towards the lingual part of the whorl. Like the previous tooth, it is also firmly attached, but the finger-like projections attaching the tooth to the base are clear.

The next three teeth are larger in size, more pointed and much more recurved than the two older ones. The teeth are becoming more S-shaped, with the tip pointing lingually and up relative to the base, as opposed to just lingually as in the two older teeth (Fig. 3.14C). The youngest of these three teeth is the largest and has the sharpest angle of recurvature.

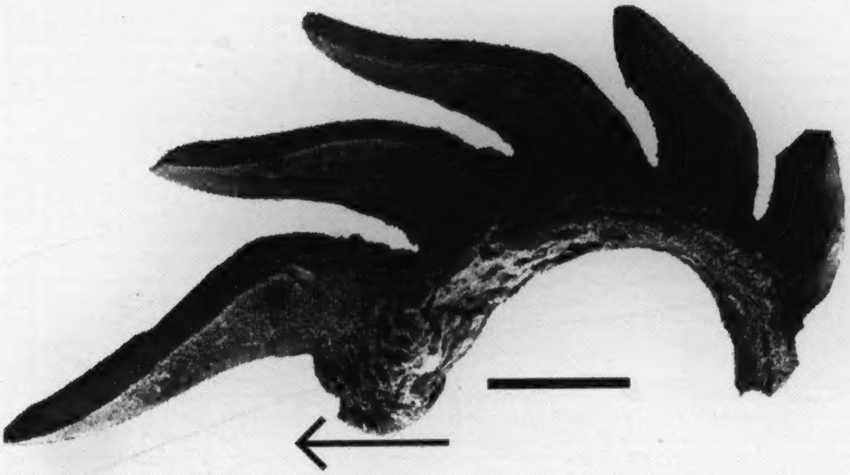

FIGURE 3.13. Gen. Nov. C et sp. nov. A, UALVP 42525, in side view. The teeth grow lingually to labially; the largest teeth are to the lingual side (left). Arrow indicates increase in thickness and width of base. Scale bar equals 1mm.

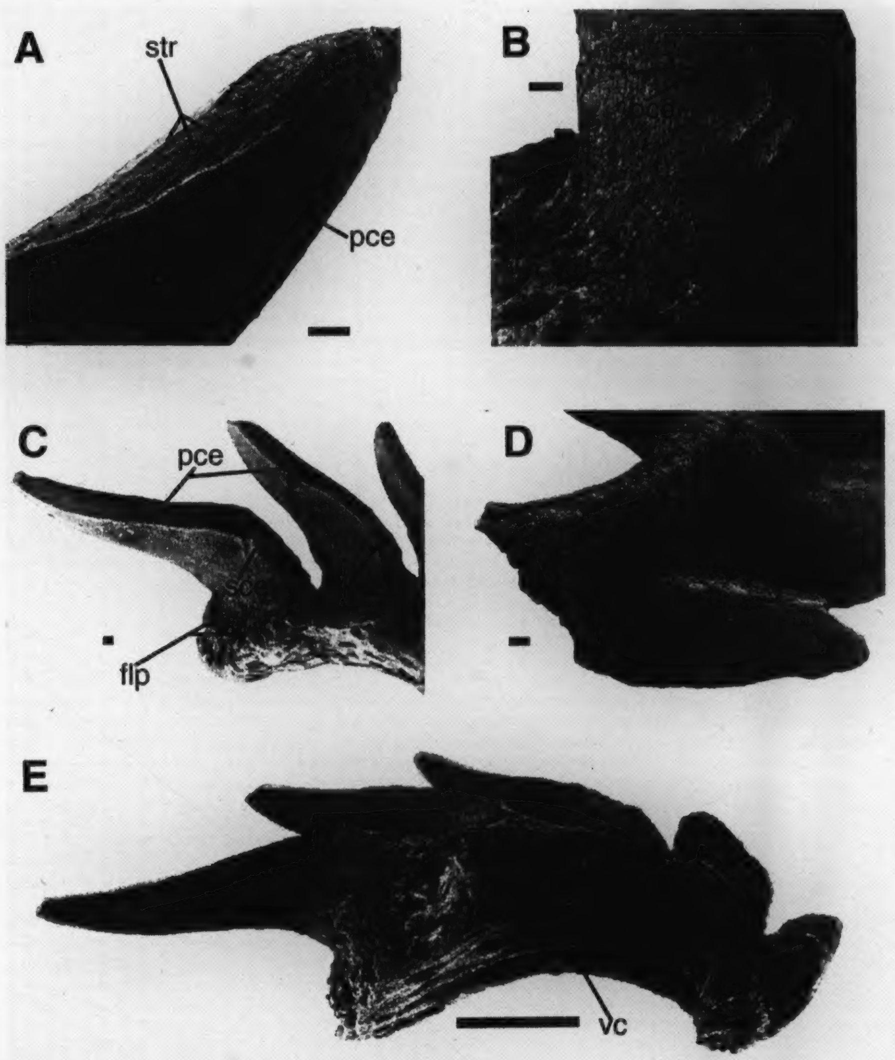

FIGURE 3.14. Gen. Nov. C et sp. nov. A, UALVP 42525. **A**, close-up of the cutting edge with the striations on the tooth above this edge; **B**, close-up of secondary cutting edges on the youngest tooth; **C**, two youngest teeth with cutting edges, showing attachment; **D**, attachment of oldest teeth to the base, more fusion of the finger-like projections; **E**, basal view, showing the vascularized canals. Scale bar of **E** equals 1mm, all others equals 100um.

These teeth have very distinct primary cutting edges on their medial sides. The primary cutting edges wrap slightly around the tooth from the labial to the lingual side. The cutting edges do not extend to the base of the tooth, but end near the greatest angle of curvature on the tooth. At the termination of the main cutting edge, there are two to three secondary cutting edges that extend off the primary cutting edges at a 45° to 90° angle posteriorly (Fig 3.14A, B, C). Above the main cutting edges, the tooth shows slight striations, parallel to the shape of the tooth. Below the cutting edges, the tooth is smooth (Fig. 3.14A).

Bases—The base of the whorl of Gen. Nov. C et sp. nov. A is similar to that of the tooth whorls of Gen. Nov. B et sp. nov. A. The base is recurved, and thickens and widens to accommodate younger, larger teeth (Fig. 3.13).

In basal view, it can be seen that the recurved base is striated with vascular canals running along it subparallel to the curvature of the base. Some of the vascular canals extend into the base of the whorl (Fig 3.14E).

Attachment of Teeth—The attachment zone of the teeth to the base of the whorl is clearly seen in all of the teeth. They are all firmly attached to the base and to each other by finger-like projections, extending from the base of the tooth. These projections do not appear to extend very deeply into the base, but they do become fused to the base and to each other (Fig. 3.14C). Although the attachment is clear in all of the teeth, the fusion of the teeth is more apparent in the older teeth than in the younger ones (Fig 3.14C, D).

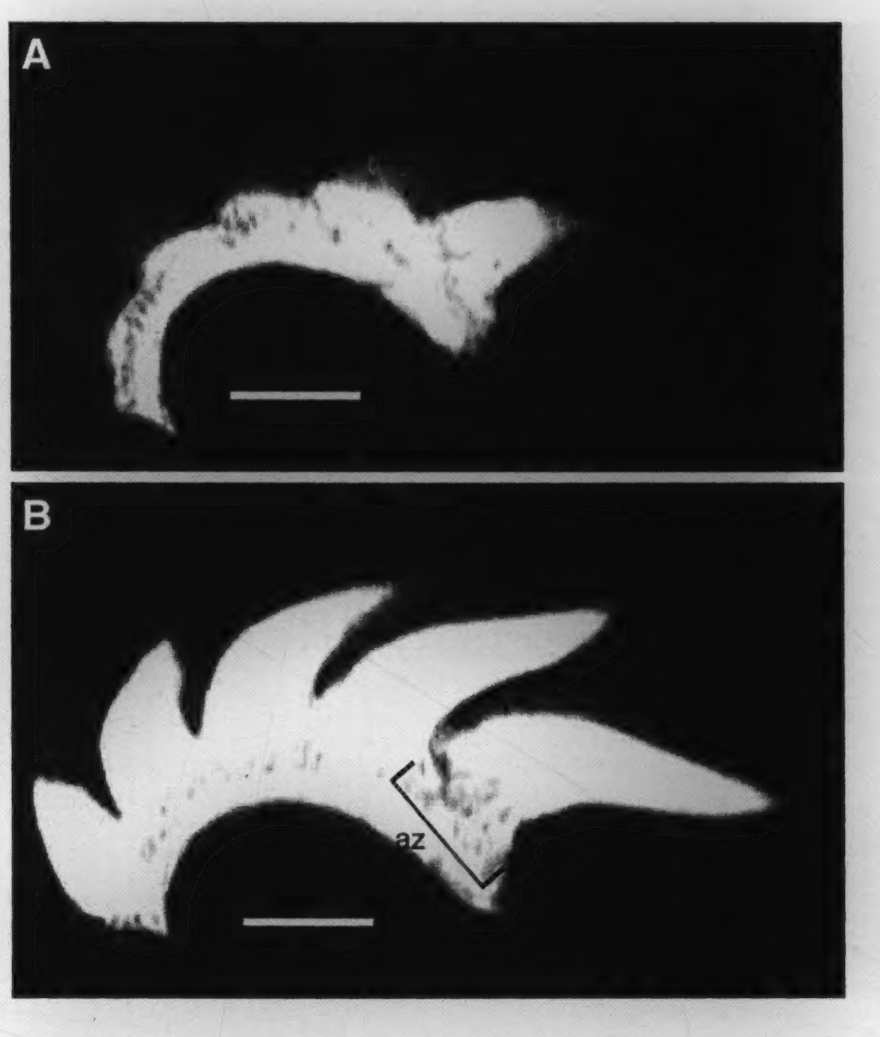

FIGURE 3.15. Gen. Nov. C et sp. nov. A, UALVP 42525, small-scale CT slices. **A**, lateral slice through the whorl, can clearly see the piggy-back attachment of the teeth to the base and each other; **B**, medial slice through the whorl, can see how the newest tooth is attaching first to the base and then to the previous tooth. Scale bars estimated to equal 1mm.

In the youngest tooth, the finger-like projections extend all of the way to the lingual end of the base. In this area, the base appears to have been still growing, to accommodate the large size of this new tooth.

The teeth, like those in the previously discussed species, are also attached in a piggy-back manner to the previous tooth. This is best seen in the two largest, youngest teeth, but can be seen to varying degrees in all of the teeth using the CT-scan data (Fig. 3.15A).

Internal Structure—CT-scan data show the vascular canals inside the tooth whorl. They extend into the base of the whorl and into the base of the teeth (Fig. 3.15B). The networking of these canals does not appear to be as extensive as that in the base of Gen. Nov. B et sp. nov B (Fig 3.9B).

There is also a network of vascular canals inside the tooth crowns of the whorl. This networking is only in the bottom third of the teeth or less, as seen by the CT-scan data. Above this area of vascularization, the teeth appear solid in the CT-scan data as well as in the smaller teeth whose tip has broken off.

Gen. Nov. C sp., cf. sp. nov A

(Fig. 3.16)

Diagnosis—Associated, isolated tooth whorls; tooth whorls large to small; large whorls with five to eight teeth; only youngest tooth well preserved; other teeth broken before fossilization, found isolated on block; teeth with primary cutting edges on lateral sides; teeth striated above primary cutting edges; small whorls with 4-5 teeth; tooth preservation varies; finger-like projections extending from all teeth onto base; bases recurved in spiral; bases and teeth vascularized; scattered scales on block, resembling scales from Gen. Nov. B et sp. nov A, to be described at a later date.

Material—UALVP 41846.01, 41846.02, 41846.03, 41846.04, 41846.05, 41846.06, 41846.07, 41846.08, 41846.09, 41846.10, 41846.11, 41846.12, 41846.13.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—This species is based on small and large isolated tooth whorls found on a block with associated scales. Because no other putative chondrichthyan material was found on the block, and because of the similarities of the elements, all of the material is considered to be associated with a single specimen.

The larger tooth whorls have a recurved base supporting five to eight teeth, the youngest of which is still intact. The smaller whorls are tiny (~2mm long) and have four to five teeth. In some of these whorls, all of the teeth are preserved, in others only the oldest tooth is preserved.

Tooth Crowns of the Large Whorls—Each large tooth whorl has five to eight teeth, of which only the youngest is still preserved on the base of the tooth whorl. Based on the broken tooth base, the teeth ranged from oval to circular in the base, and grew larger with the addition of each tooth (Fig. 3.16A).

The youngest teeth are more oval in the base and are recurved to point in the lingual direction. On the labial side, the tooth broadens and is somewhat flattened. This flattened part of the tooth is defined by primary cutting edges.

These cutting edges wrap around the teeth from the labial side to the lingual side, and are more recurved than the tooth. There are no secondary cutting edges in these tooth whorls, and the primary cutting edges end around two-thirds of the way down the tooth crown (Fig. 3.16A, D). As in Gen. Nov. C et sp. nov A, the teeth are striated above the primary cutting edges (Fig. 3.16C).

On the block that the tooth whorls are from, several isolated, broken teeth of the tooth whorls were recovered. It is evident that the teeth are from the tooth whorls because they have the same morphology as the youngest teeth still preserved on the whorls. These teeth are important because they may give important information about ontogeny and the growth of the tooth whorl (Fig. 3.16C, D).

These isolated teeth vary in size and slightly in shape as would be expected from the oldest to youngest teeth. The smaller teeth are pointed and do not recurve much, and are believed to correspond to the older teeth. The larger teeth have more defined primary cutting edges and are recurved; these are believed to be the younger teeth (Fig. 3.16D).

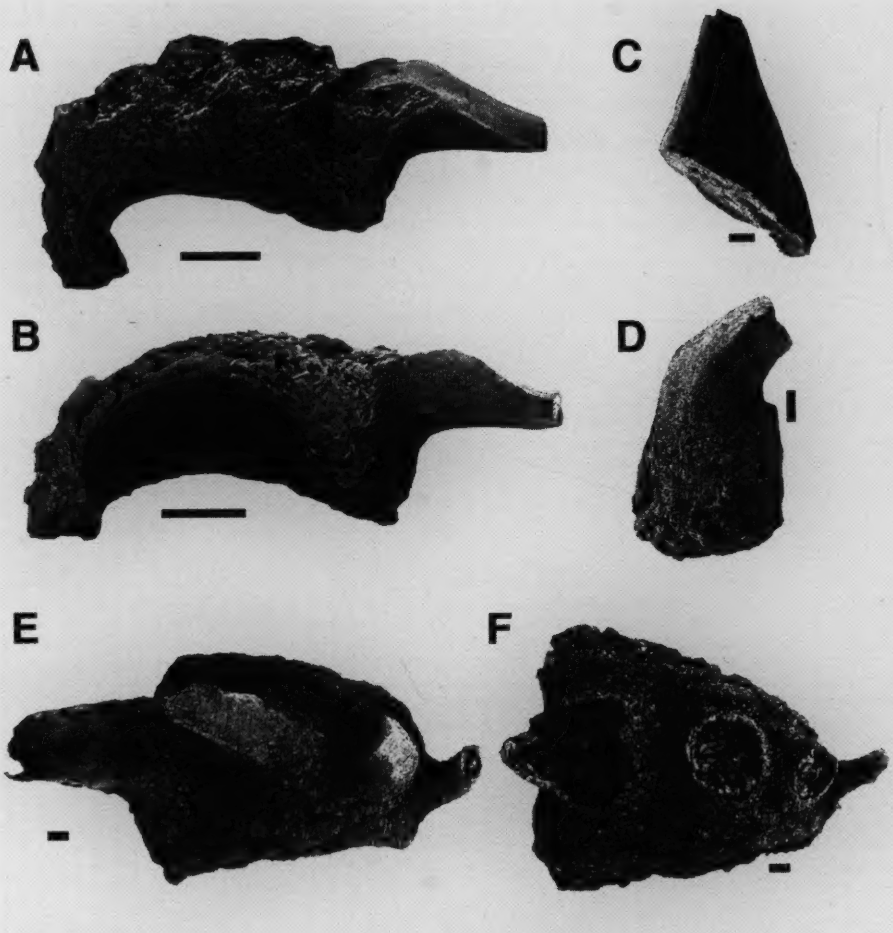

FIGURE 3.16. Gen. Nov. C cf. sp. nov. A, SEM images of assorted tooth whorls and shed? teeth from UALVP 41864. **A**, UALVP 41864.01, tooth whorl in side view, lingual is right; **B**, UALVP 41864.01, tooth whorl in basal view, lingual is right; **C**, UALVP 41864.13, broken tooth; **D**, UALVP 41864.12, broken tooth; **E**, UALVP 41864.05, small tooth whorl in crown view, lingual is left; **F**, UALVP 41864. 04, small tooth whorl in crown view, ligual is left. Scale bars for **A**-**B** equal 1mm, all other scale bars equal 100um.

Bases of the Large Tooth Whorls—The bases of the large tooth whorls are very recurved and highly vascularized in side and basal view. Like the other tooth whorls discussed in this chapter, the bases increase in thickness as larger teeth are attached, but they thicken very quickly as the new teeth are added (Fig. 3.16A).

These tooth whorls have very recurved bases and the oldest part of the whorl is often found tightly tucked directly under the youngest tooth. This is only seen in some of the specimens; in most of the tooth whorls, the oldest part of the base with teeth has been broken off (Fig. 3.16B).

Tooth Crowns of the Small Whorls—The smaller tooth whorls found associated with the scattered material are very similar in morphology to the larger whorls, but they do not seem to lose teeth as readily. Two of these small whorls have been removed and prepared for a better understanding of their morphology. One of the tooth whorls is intact while the other has lost all of its teeth except the oldest one (Fig. 3.16E, F).

In the intact whorl, there are four curved, pointed teeth, facing the lingual direction. All of the teeth are rounded to sub oval in their base and become rounded in the crown. They all share a similar morphology and only increase in size as the younger ones are added (Fig. 3.16E).

In the other small whorl, only the oldest tooth is still preserved on the base. Three of the teeth have broken off, or fallen off before fossilization. The bases of the teeth are round and show a great deal of vascularization (Fig. 3.16F).

The teeth are smooth and do not have any striations. There are small primary cutting edges along the lateral sides of the teeth. These cutting edges run along the teeth from the tip to the base. There is evidence for at least one secondary cutting edge coming off the labial side of the primary cutting edge just above the base of the tooth. This was seen in a larger tooth of a broken small whorl, and the secondary cutting edges are assumed to be present in at least all of the larger teeth of the smaller whorls.

Bases of the Small Tooth Whorls—The bases of the small whorls are recurved and highly vascularized, as seen in the large whorls of the species. The smaller bases do not thicken as much to accommodate the larger teeth as do the larger whorls. The bases of the small whorls are much more triangular in shape and widen very rapidly with the addition of the younger, larger teeth (Fig. 3.16E, F).

Attachment of the Teeth—As in Gen. Nov. C et sp. nov. A, there are finger-like projections attaching the teeth to the base of the tooth whorl in both the large and the small tooth whorls. In the larger tooth whorls, even though all but one of the teeth has been broken off, it is still evident that the teeth were attached in the same piggy-back style as the other putative chondrichthyans in this chapter (Fig. 3.16A). This is less clear in the smaller tooth whorls; the teeth are spaced much farther from each other than in the larger teeth (Fig. 3.16E). Thin-sectioning of some of the tooth whorls would be helpful in better understanding the attachment of the teeth to their bases and understanding if there is a difference between the larger and smaller whorls.

Internal Structure—Although I do not have any CT-scan data or thin-sections for this species, it is assumed that the histology is similar to that of Gen. Nov. C et sp. nov. A.

From the tooth whorls of Gen. Nov. C sp. cf. sp. nov. A, it is very evident that the bases of the whorls were highly vascularized. This vascularization can be at least extended into the bases of the teeth, based on missing teeth on the large and small tooth whorls (Fig. 3.16). It also appears that the vascular canals extend quite a bit into the teeth, as seen in the damaged areas of the large and small teeth that are still in situ (Fig. 3.16A, E). Thin sectioning would also help to give a better understanding of the histology of these tooth whorls.

Remarks—In most cases, only the youngest teeth are fossilized attached to the base of the large tooth whorl. This suggests that the teeth were either broken off or dropped off before preservation, perhaps even during ontogeny; the base where the teeth are missing does not show evidence of recent breakage (there is no change in the texture of the base). It is possible that the teeth in this species were only loosely attached to the base by ligaments and did not become completely fused like the teeth in the other species discussed in this chapter.

In the small tooth whorls, the teeth are more firmly attached to the base and do not appear to have been lost or shed. In the case where only one of the teeth was left on the whorl, it appears that the teeth were broken off the whorl instead of begin lost or shed like those seen in the larger tooth whorls of the same species.

Gen. Nov. C et sp. nov. B

(Fig. 3.17-3.19)

Diagnosis—Putative chondrichthyan based on tooth whorl with base recurved in spiral; thirteen or more teeth, pointed, fused to base; tooth size increasing lingually; larger teeth facing lingually; cutting edge more recurved than tooth; secondary cutting edges arising from both sides of primary cutting edge; teeth smooth above cutting edge; base thickening with addition of larger teeth; tooth attachment loose by finger-like projections; teeth with piggy-back attachment; base and bottom of teeth vascularized.

Material—UALVP 41664, 47221.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—Both specimens belonging to Gen. Nov. C et sp. nov. B consist of isolated tooth whorls, found with no other associated material. These whorls are similar to those belonging to Gen. Nov. C et sp. nov. A in that they consist of a recurved base with a single row of recurved teeth. However, in this species, the base is recurved into a spiral and the number and morphology of the teeth differ greatly (Fig. 3.17).

Tooth Crowns—There are thirteen teeth preserved on UALVP 41664 and eleven preserved on UALVP 47221, although the oldest part of this tooth whorl has been broken and it is unclear how many other teeth it possessed.

The older teeth are small and rounded; this is best seen in the three oldest preserved teeth in UALVP 47221 (Fig. 3.19B). The teeth are not very tall, but increase in height lingually. In crown view, the teeth are oval and are flat-topped, and not pointed, possibly indicating wear of the tooth. These teeth are not tightly packed together.

Moving lingually along the tooth whorl, the teeth become larger, more pointed, and begin to become recurved, facing lingually. This directionality can be first seen in the third to oldest teeth in UALVP 41664 (Fig. 3.18A) and UALVP 47221 (Fig 3.19A). As the teeth increase in size, the primary and, eventually secondary cutting edges also appear on the youngest teeth.

The three largest, youngest teeth are the most intact and the morphology can be clearly seen. These teeth are recurved towards the lingual end of the whorl and are progressively larger, in that direction. The bottoms of these teeth are larger and wider than those of the older teeth. The larger teeth are more closely packed together than the smaller, more rounded ones. This may be due in part to the piggy-back type of attachment (Fig 3.19A).

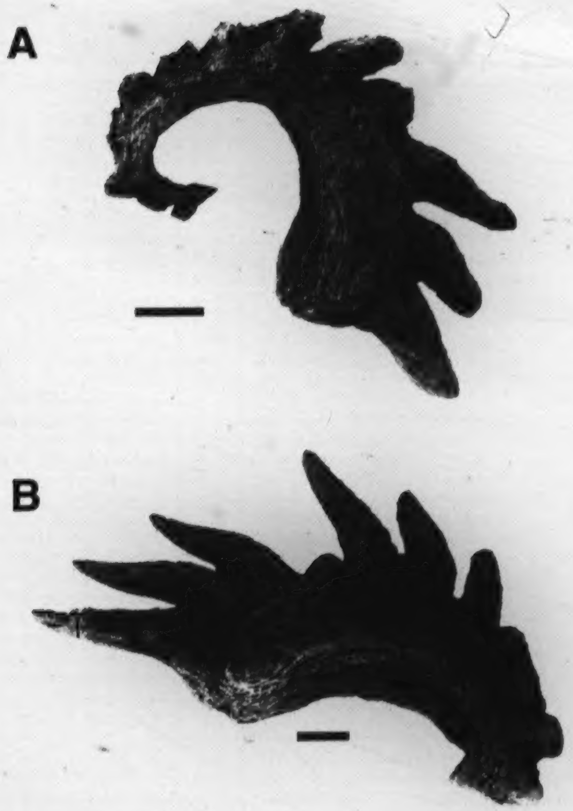

FIGURE 3.17. Gen. Nov. C et sp. nov. B. **A**, UALVP 41664 (holotype), in side view, the lingual direction is to the right; **B**, UALVP 47221 (image pieced together from 2 SEM images) in side view, the lingual direction is to the left. Scale bars equal 1mm.

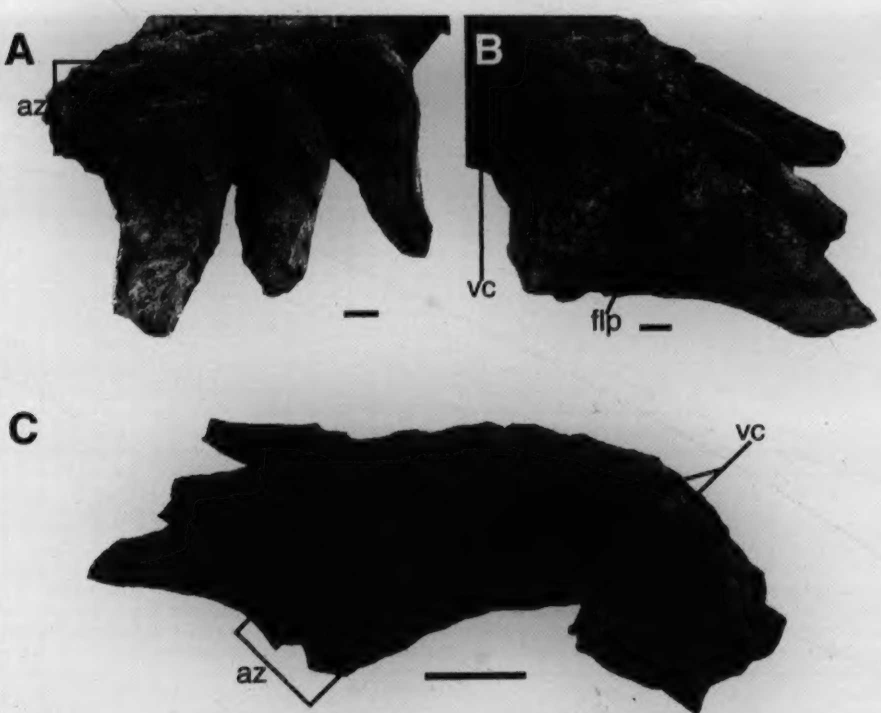

FIGURE 3.18. Gen. Nov. C et sp. nov. B, UALVP 41664. **A**, the three youngest teeth; **B**, youngest tooth from the lingual side, note the tooth is not quite attached to the base; **C**, basal view, showing the vascular canals. Scale bars for **A**-**B** equal 300um, scale bar for **C** equals 1mm.

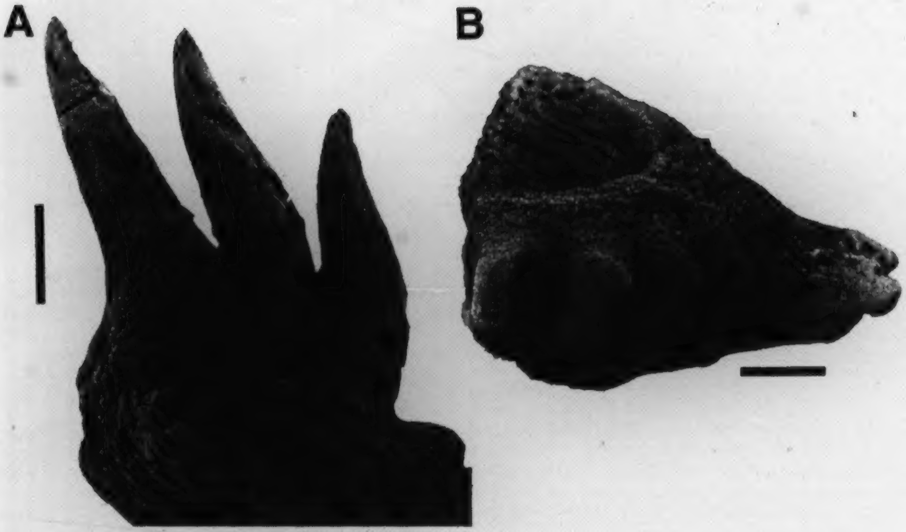

FIGURE 3.19. Gen. Nov. C et sp. nov. B, UALVP 47221. **A**, three youngest teeth, closely packed and attached to the base and piggybacked on older teeth; **B**, three oldest teeth, rounded with flat top. Scale bars equal 1mm.

As in Gen. Nov. C et sp. nov. A, there are primary cutting edges along the lateral sides of the teeth and these have accessory edges as well. The primary cutting edges follow the curvature of the tooth. At the bottom of these primary cutting edges, there are three to four secondary cutting edges that arise from the posterior and anterior sides of the primary edges at ~35° (Fig. 3.18A).

Bases—The base is largely recurved in a spiral. The base both thickens and widens as it spirals out to accommodate the larger, wider, younger teeth (Fig. 3.17, Fig 3.18C).

In basal view, vascular canals can be seen running along the base of the whorl. Some of these extend all the way from the oldest part of the whorl to the youngest. They do not run parallel to the sides of the base, but rather diagonally from one side to the other (Fig. 3.18C).

Attachment of the Teeth—In side view, the base appears mostly solid and continuous, but the attachment zones of the youngest teeth to the base can be seen (Fig 3.18A, C). Like the other putative chondrichthyan tooth whorls discussed in this chapter, the teeth are piggy-backed onto each other, with finger-like projections attaching the tooth to the base (Fig 3.19A).

Internal structure—From CT-scan data, the vascular canals can be traced through the base of the whorl and into the tooth crowns. Unlike Gen. Nov. C et sp. nov. A, the vascular canals extend into more than just the base of the teeth. From the scans, it is also evident that the main canals are connected to each other and the teeth via shorter canals.

The piggy-back attachment of the teeth is also evident, and the finger-like projections appear to attach deeply into the base of the whorl. This attachment is clearer in the younger teeth, as the fusion is not as complete as in the older teeth (Fig. 3.18; Fig. 3.19).

Gen. Nov. D

Gen. Nov. D et sp. nov. A

(Fig. 3.20-Fig. 3.22)

Diagnosis—Putative chondrichthyan based on an isolated tooth whorl; base recurved, more open; fourteen teeth fused to base; oldest teeth small, rounded; middle teeth V-shaped with keel fitting into notch of next tooth; youngest teeth larger, recurved, with lateral cutting edges; youngest tooth not fully attached to base; base thickening with younger teeth; base and teeth heavily vascularized.

Material—UALVP 47083.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Description—UALVP 47083 is an isolated tooth whorl, with no associated body material. There are fourteen total teeth on this whorl that are mostly intact. This tooth whorl is almost complete and is very well preserved, making the variation in teeth apparent. The base is recurved and the teeth vary from small and rounded in shape, to V-shaped, to pointed, going from oldest to youngest tooth. There is only one row of teeth, but unlike the two previously described tooth whorls, the teeth of Gen. Nov. D et sp. nov. A vary greatly from oldest to youngest (Fig. 3.20).

Tooth Crowns—The oldest two to three teeth are the smallest and are rounded to oval. They are low to the base and are very closely packed together (Figs. 3.20A, 3.21D).

The next six teeth gradually become V-shaped and begin to widen and grow upward, becoming more pointed. The notches of the V's point lingually, towards the newer teeth. In side view, it can be seen that at the point in the V, there is a keel that extends into the notch of the V on the next younger tooth. As the teeth get younger, the sides of the teeth become longer and the base of the V becomes elongated and flattened out (Fig. 3.21).

The following two teeth are transformational teeth between these V-shaped teeth and the youngest, pointed teeth. These two teeth still have large keels facing lingually and a notch opening labially, but they are much more pointed and are slightly recurved (Figs. 3.20, 3.21C).

The three youngest teeth are less closely packed than the rest of the teeth and have primary cutting edges on their sides. The keel becomes small and is lost in the youngest teeth. These teeth are no longer V-shaped, and the labial side of the tooth is smooth and flat. The teeth become slightly recurved lingually and are much wider and longer than the remaining teeth (Figs. 3.20A, 3.21A).

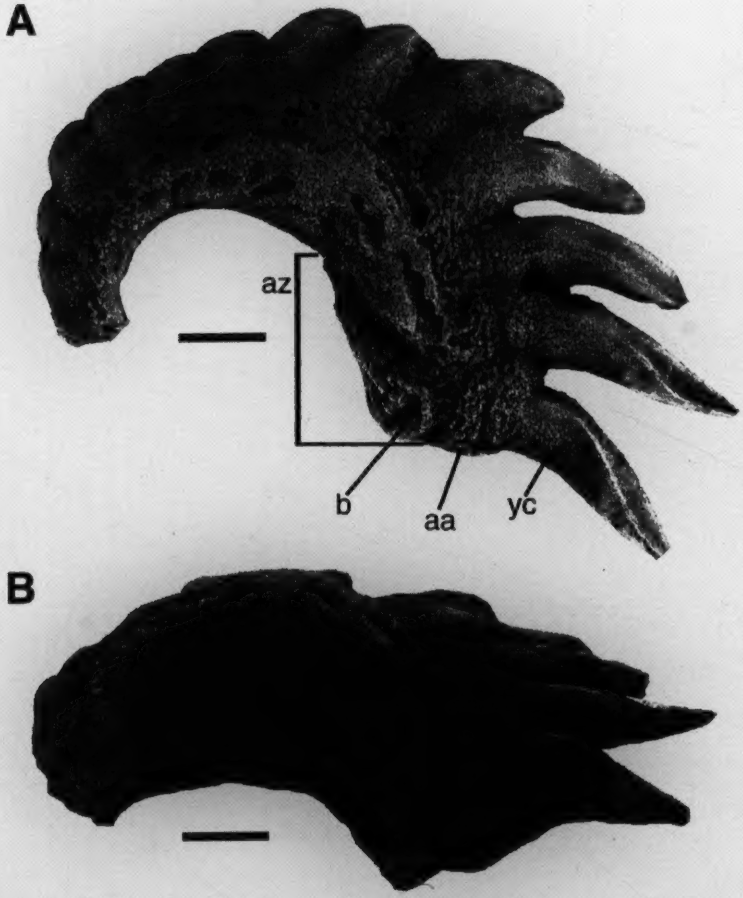

FIGURE 3.20. Gen. Nov. D et sp. nov. A, UALVP 47083 (holotype), in side view, showing the three layers of attachment of the youngest tooth (the new base, the intermediate area of attachment, and the tooth crown)(**A**), and in basal view (**B**); lingual is right. Scale bars equal 1mm.

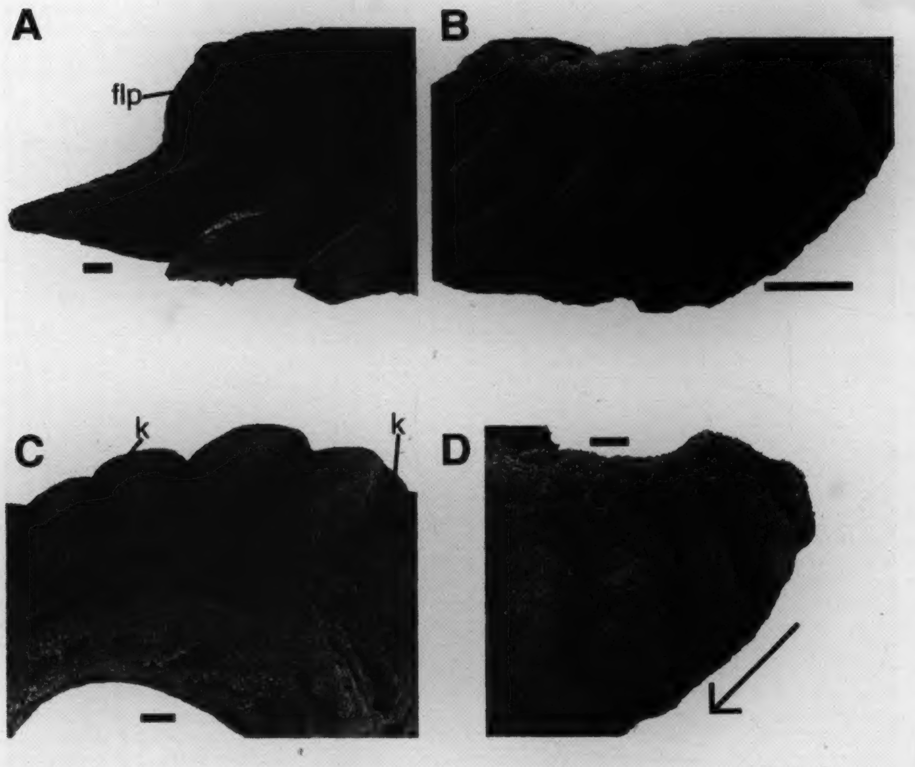

FIGURE 3.21. Gen. Nov. D et sp. nov. A, UALVP 47083. **A**, crown view of three youngest teeth, showing finger-like projections and piggy-back attachment; **B**, crown view of middle, V-shaped teeth; **C**, side view of middle V-shaped teeth, showing the keel on the lingual side of the tooth; **D**, crown view of oldest teeth, showing transition from rounded to V-shaped teeth (arrow indicates lingual direction). Scale bar for **B** equals 1mm, all others equal 300um.

Bases—The base of this whorl thickens with the addition of larger teeth and under the youngest tooth is almost as thick as the height of the tooth it supports. There is a great deal of vascularization visible on the side of the tooth whorl, in addition to the bottom (Fig. 3.20).

In basal view (Fig. 3.20B), a series of canals and grooves are visible along and extending into the base of the whorl. The base is very wide throughout the whorl and only widens slightly to accommodate larger teeth.

In this tooth whorl, the youngest tooth was preserved in the process of becoming attached to the rest of the base, and this can be clearly seen in both side and basal view (Fig. 3.20). The tooth and the new portion of the base were becoming attached to the base at the same time, as can be seen by the broad attachment zone.

Attachment of the Teeth—The mechanism of tooth attachment appears to be similar to that of the other putative chondrichthyans discussed in this chapter. I am able to make more observations about the method of attachment and the zones of attachment because the youngest tooth was in the process of becoming attached to the rest of the tooth whorl.

In this area of the whorl, there appear to be three distinct layers being added consecutively; a layer of new base, the area of the tooth attachment, and an intermediate area of attachment. From this youngest tooth, the area of attachment of the tooth to the rest of the base can be roughly traced beneath the rest of the teeth to the base of the whorl.

The new, attaching layer of the base extends far labially, beneath the next three youngest teeth. Although the attachment and fusion of the youngest tooth and its underlying base do not appear to be complete, they are already very firmly attached to the rest of the base. This process of attachment greatly differs from that seen in the previous three species.

The labial four to five teeth do seem to be slightly piggy-backed, as seen in some of the other whorls discussed. There is also evidence for similar types of finger-like projections coming off the bottom of each tooth, attaching it to a part of the base (Fig. 3.20A). The other nine to ten teeth appear to be closely packed together, with keel-in-notch interlocking of the V-shaped teeth.

Internal structure—CT-scan data indicated a great deal of vascularization in the base of the tooth whorl, extending into and throughout the teeth (Fig. 3.22). In different slices of the CT-scan, the vascular canals can be seen extending throughout the tooth whorl, and their connections can be better understood.

The different areas of attachment, base, middle, and tooth also appear to persist throughout the rest of the whorl. Although, externally, the youngest tooth has not yet become fully fused to the rest of the whorl, the vascular canals extend from the old into both the new tooth and base.

With the CT-scan data, it is also clearer that at least the four to five youngest teeth did have a piggy-back attachment (Fig. 3.22A, B). The resolution

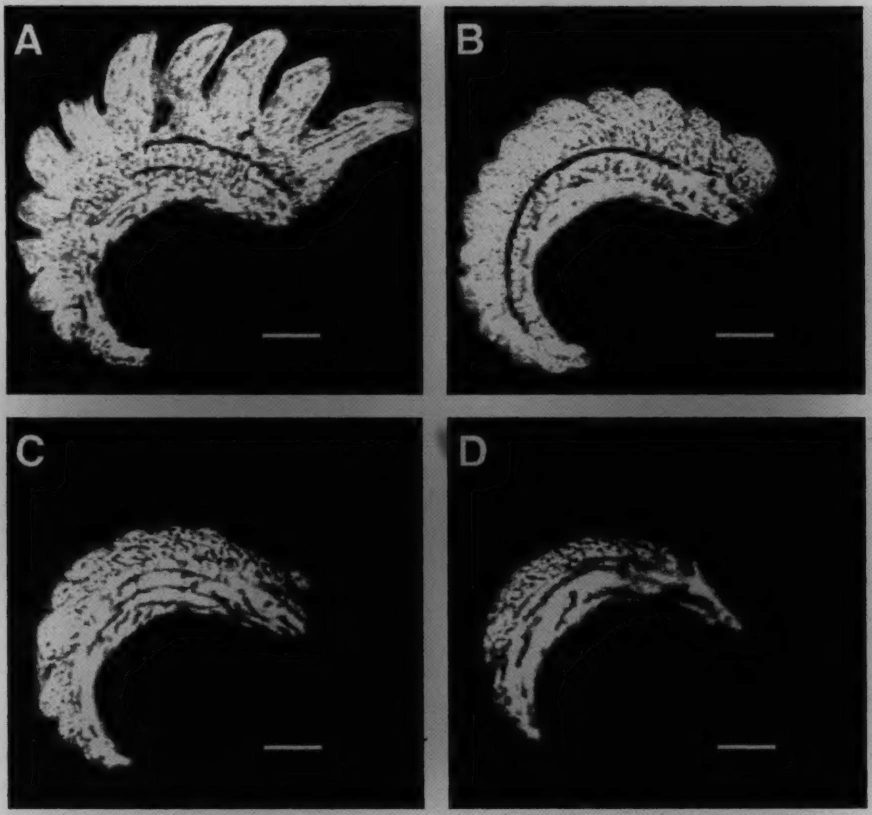

FIGURE 3.22. Gen. Nov. D et sp. nov. A, UALVP 47083, CT-scan slices. **A**, medial slice (087), showing vascularization of the base and the teeth as well as the piggy-back attachment of the teeth; **B** (138), **C** (155), and **D** (164), lateral slices through the whorl, showing different views of the vascularized canals. Scale bars estimated at 1mm.

is not sufficient for me to make assumptions about the attachment of the older teeth, but I assume it is similar to what is seen in the younger teeth.

Class ACANTHODII Owen, 1846
Order "CLIMATIFORMES" Berg, 1940
Suborder BROCHOADMONOIDEI Gagnier and Wilson, 1996
Family BROCHOADMONIDAE Bernacsek and Dinely, 1977
Genus *BROCHOADMONES* Bernacsek and Dineley, 1977
BROCHOADMONES MILESI Bernacsek and Dineley, 1977
(Fig. 3.23-Fig 3.26)

Revised Diagnosis—This is a diagnosis for the dentition and associated structures of *Brochoadmones milesi*. For other diagnostic features, see Hanke and Wilson (2006). Tooth whorls lining upper and lower jaw margins; tooth whorls smallest at back of gape, largest at front; whorls growing lingually to labially; medial row of teeth pointed, persisting beyond lateral rows; lateral teeth spatulate; Meckel's and palatoquadrate cartilages unossified; larger tooth whorls near symphysis of upper and lower jaws; tooth-like branchial denticles arranged in tooth families in branchial region, below otic capsules.

Remarks—*Brochoadmones milesi* was first described by Bernascsek and Dineley (1977), based on a poorly preserved specimen with spines, scales and four tooth whorls. It was then redescribed with more complete fossil data by Gagnier and Wilson (1996), and was most recently revised by Hanke and Wilson

(2006). This current description is limited to the tooth whorls and branchial denticles. For a description of the overall morphology, see Hanke and Wilson (2006).

Holotype—NMC 22710.

Material—Body specimens with dentition: UALVP 32399, 32672, 39054, 41490, 41490, 41494, 41495, 42154, 43028, 47959; isolated whorls: UALVP 41708, 43098; pharyngo-denticles: UALVP 32399, 32406, 32672, 41490, 41495, 43028, 47241; for additional specimens, see Hanke and Wilson (2006).

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—The tooth whorls of *Brochoadmones milesi* line the upper and lower jaw margins and grew lingually to labially. This condition is only seen in some of the articulated specimens (Fig. 3.23A, B, D); it appears that in most of the specimens, the whorls shifted during preservation, probably because they were not firmly attached to the jaw cartilages. In some specimens, where the whorls are preserved in-situ, there are also larger whorls (at least two) at the presumed location of the symphysis between left and right Meckel's and palatoquadrate cartilages. These whorls are larger than the ones lining the jaw margins, but are otherwise identical in structure (Fig 3.23C).

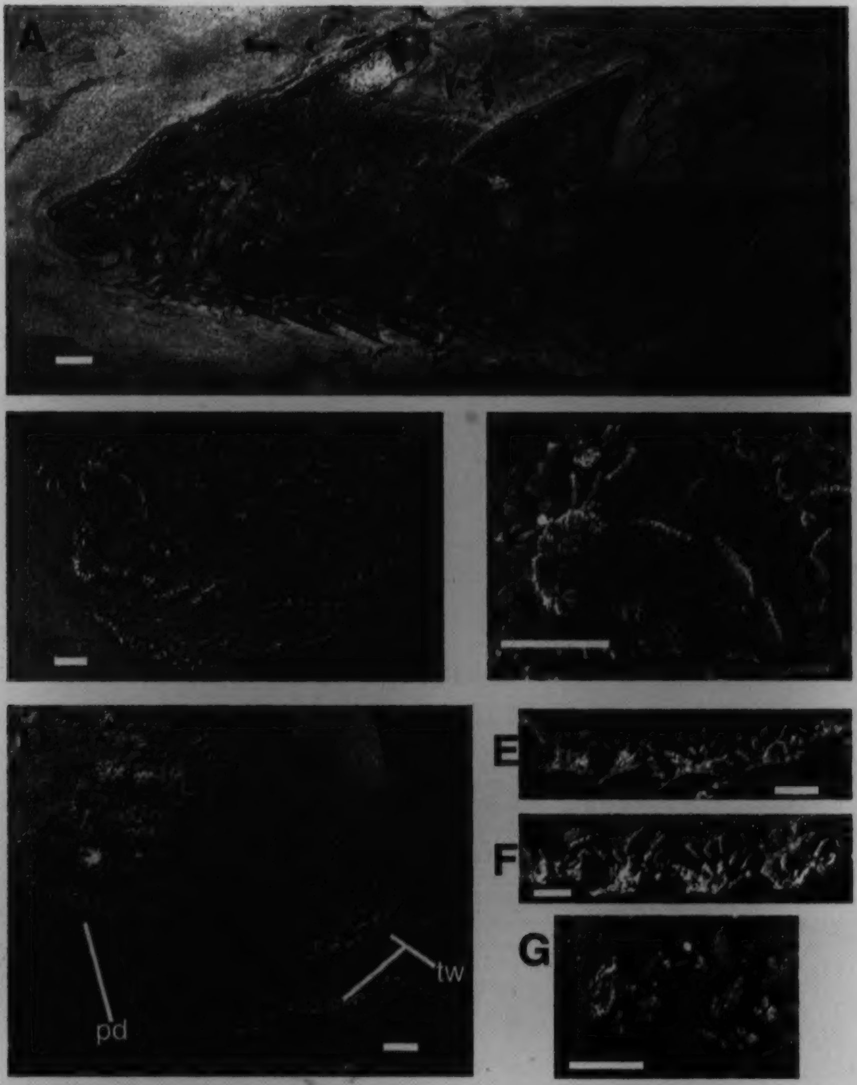

FIGURE 3.23. *Brochoadmones milesi*, **A**-**C**, UALVP 41495, **D**-**G**, UALVP 32672. **A**, an almost perfectly preserved specimen; **B**, close-up of the mouth, upper and lower tooth whorl rows; **C**, larger (symphyseal?) upper tooth whorls; **D**, head of *B. milesi* with tooth whorls lining upper and lower jaw margins; **E**, lower jaw margin tooth whorls in side view; **F**, lower jaw margin tooth whorls in crown view; **G**, leaf-shaped pharyngo-denticles. Scale bars for **A**,**D** equal 1cm, scale bars for **B**,**C** equal 1mm, scale bars for **E**-**G** equal 0.5mm.

Each tooth whorl consists of a thin, recurved base that generally supports three rows of teeth, which, during later development, change shape and become arranged in a single row. Based on the position of the in-situ whorls in some of the full body specimens, I am able to confirm the position of the whorls in the mouth as well as to suggest which teeth are oldest and which are the youngest (Fig 3.23E, F).

Tooth Crowns—The oldest teeth are situated in three rows that are slightly oblique to the midline of the base of the whorl. The two outside rows are made up of five to seven teeth each. These teeth are spatulate, with three points along the edge of each blade; the spatulate teeth are, like the row itself, also facing slightly oblique to the central, medial axis of the whorl (Fig. 3.24).

The medial row of teeth follows the same alignment as the two lateral rows, but the teeth differ in morphology and number. This row contains six to nine conical teeth, depending on the size of the tooth whorl. The teeth are sharp and directed lingually, into the oral cavity. They also increase in size much more rapidly than the spatulate teeth as the medial row of teeth develops, while the lateral ones do not change very much in size.

The teeth on the tooth whorls of *B. milesi* grow asymmetrically, making the older rows of teeth oblique to each other and to the base of the whorl, giving the tooth whorls a slanted appearance. The orientation of the asymmetry varies in different tooth whorls. In the specimens where the tooth whorls are in situ, the

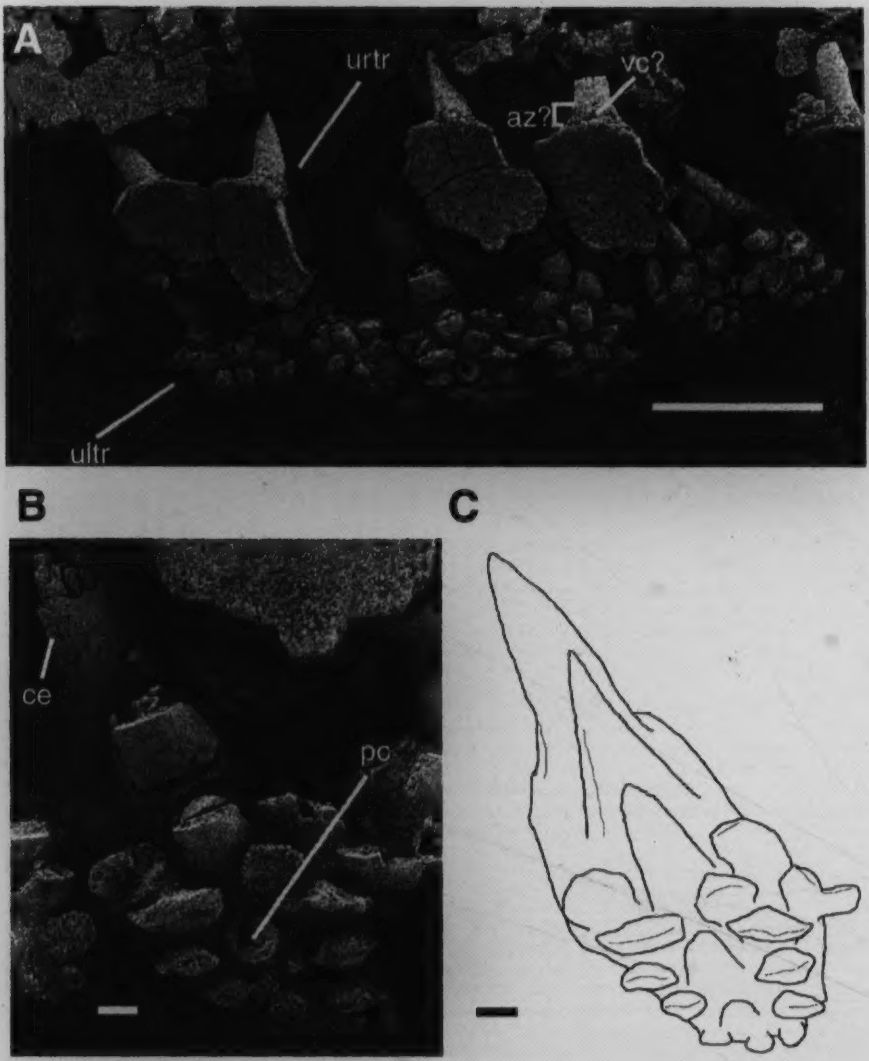

FIGURE 3.24. *Brochoadmones milesi* (UALVP 41708). **A**, two rows of tooth whorls (left and right upper), anterior is to the right; **B**, tooth whorl, lingual is to the upper left; **C**, reconstruction of the tooth whorl seen in **B**. Scale bar for **A** equals 1mm, all other scale bars equal 100um.

asymmetry appears to correspond to directionality of the corresponding jaw margin.

Bases—The base of each whorl in *B. milesi* is only slightly curved, and very thin. This condition is different from that seen in the putative chondrichthyans previously discussed in this chapter. Although some of the fishes may be comparable in size, the tooth whorls of *B. milesi* are also comparatively much smaller than those seen in the putative chondrichthyans.

In UALVP 32672, the tooth whorls have shifted slightly and the bases of the whorls can be seen in side view. The lingual side of the base of the whorl is flat and extends beyond the youngest tooth, suggesting that the base had been growing before the development of the teeth (Fig 3.23E).

The bases are not only very thin but they also do not increase in thickness, but only in width, as larger teeth are added, making them very different from the bases of the putative chondrichthyan tooth whorls. This could be functionally related to the hollowness of the teeth making them lighter, and thus more easily supported by the thinner base.

In basal view, the base of each tooth whorl is smooth and shows no obvious evidence of vascularization. There are no prominent canals running along the base or into it; this is also very different than what was seen in the tooth whorls of putative chondrichthyans discussed in this chapter (Fig. 3.24A).

Attachment of the Teeth—The mode of attachment of these teeth to their base is not as clear as that seen in the previously discussed putative chondrichthyans (see above). The teeth are very firmly attached to their base and there is a lack of evidence showing clear attachment zones for most of the teeth.

In some of the specimens, there is a slight indication of what may be an attachment zone. This is only seen in the youngest, newest teeth that have not had the chance to become completely fused to the rest of the whorl. In these specimens, there is an area that does not appear to be as mineralized as the rest of the tooth and base and there is some evidence for vascularization, possibly associated with the attachment of the tooth to base (Fig. 3.24A).

Internal Structure of the Tooth Whorls—The teeth are hollow and have a single, continuous pulp cavity. This is evident when looking at the broken teeth in many of the specimens (Fig 3.24B). Based on this type of observation, the teeth of both the medial and lateral rows appear to have a single, main pulp cavity.

Due to their small size and delicate structure, making the tooth whorls difficult to extract from the matrix, I was unable to have thin sections made. For the same reasons, the resolution of the small-scale CT scanner was not high enough to capture good histological images. Therefore, I do not have much histological data from the tooth whorls of *B. milesi*.

The similar structure of these whorls to those of other acanthodians leads me to believe that their histology would also be similar. This type of histology is described in some detail in the *Ischnacanthus* portion of this chapter. For more detailed information on the histology of acanthodian tooth whorls, see Gross (1971).

Symphyseal Tooth Whorls—The symphyseal tooth whorls are similar in morphology to the tooth whorls lining the jaw margins, but are about twice the size. There are two to three of the larger whorls located in the upper and lower jaw symphyseal positions.

There is a great deal of size difference between the tooth whorls lining the jaw margins and the ones at the symphysis; this is best seen in UALVP 47959. Although this is not the best preserved specimen, the upper and lower right tooth rows can be seen in situ, as well as the more anterior, symphyseal tooth whorls. Seen in place, the symphyseal whorls are clearly larger than the others (Fig. 3.25A).

UALVP 47959 is a smaller specimen of *Brochoadmones milesi*, and it is possible that it was a juvenile, explaining the smaller, less developed tooth whorls lining the jaw margins (Fig 3.25D, E). The large size and amount of development of the symphyseal whorls shows how large they are in comparison to the whorls lining the jaw margins. It is possible that this variation of development between the larger symphyseal tooth whorls and the smaller marginal whorls may have helped with a transition of different feeding styles. To understand better the morphology of the different tooth whorls, several were extracted from the upper jaw margin, as were two at the mandibular symphysis. After further preparation and SEM analysis, it is clear that there is a large size difference between the two

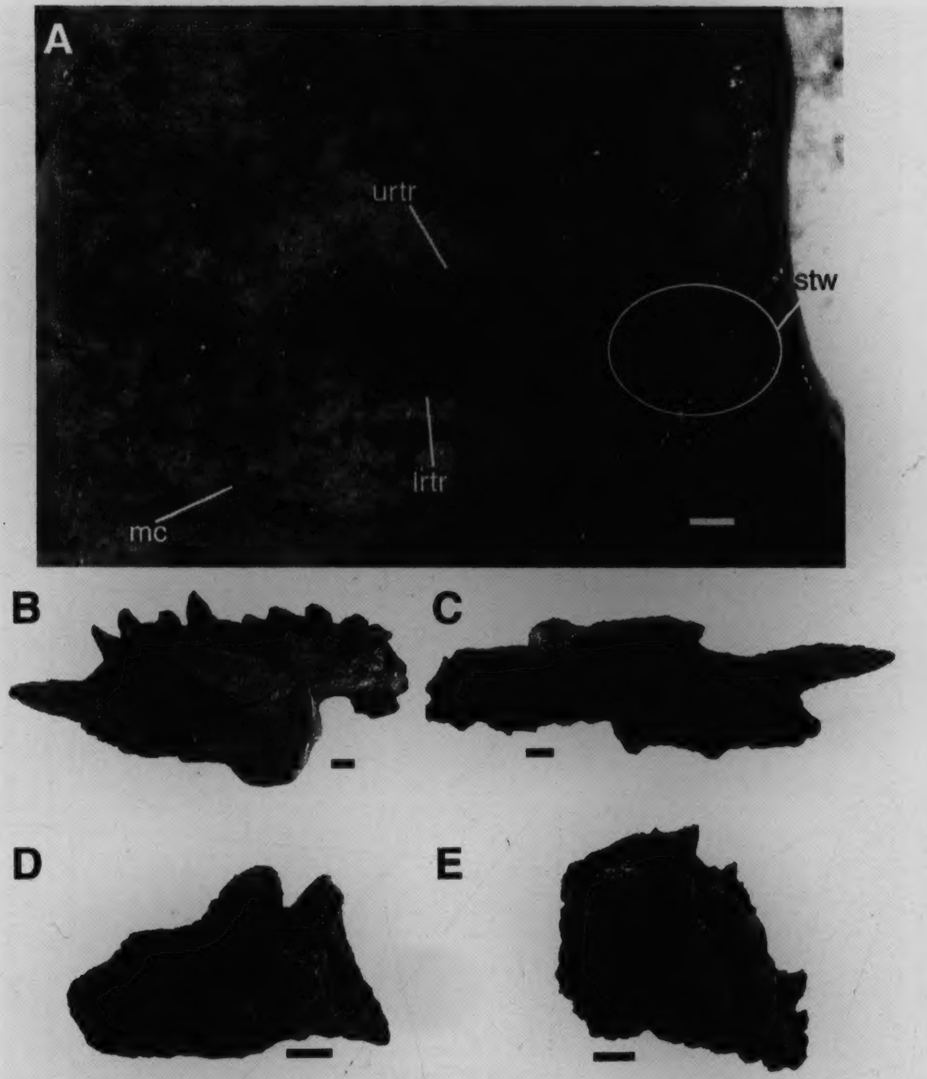

FIGURE 3.25. *Brochoadmones milesi* (UALVP 47959). **A**, head of *B. milesi* with specialized dentitions noted; **B**, UALVP 47959.01, symphyseal tooth whorls in side view; **C**, UALVP 47959.01, in crown view; **D**, UALVP 47959.03, upper tooth whorl in crown view; **E**, UALVP 47959.04, upper tooth whorl in crown view. Scale bar of **A** equals 1mm, all other scale bars equal 100um.

types of tooth whorls. The symphyseal tooth whorls have more medial and lateral teeth than the tooth whorls lining the jaw margins (Fig 3.25B, C).

Pharyngo-denticles—The pharyngo-denticles were first noted by Gagnier and Wilson (1996), and were referred to as 'gill rakers'. In their newest revision of *B. milesi*, Hanke and Wilson (2006) did not think there were branchial denticles at all. They discussed the denticles described by Gagnier and Wilson (1996) as "isolated, tiny whorl-like denticles" in the pharyngeal area of the fish, but said "given the rarity of these denticles, it is possible that they represent small, posteriorly displaced tooth whorls rather than pharyngeal teeth." I believe that these structures are pharyngeal teeth, or denticles, based on their common morphology and occurrence in many of the specimens of *B. milesi*.

The pharyngeal denticles are found in the anterior part of the branchial region, usually clustered under the otic sandy infilling. They are much smaller than tooth whorls, and differ greatly in morphology. It is possible that they are a specialized type of tooth whorl that has migrated, during the evolutionary history of the lineage, to the pharyngeal region of the oral cavity.

The denticles are leaf shaped and somewhat conical. There is generally a central denticle with two or, sometimes in the larger denticles, four lateral denticles (Fig. 3.26B). The denticles seem to be grouped in families, similar to those seen in the tooth whorls, and it is plausible that the schematics of the denticles drawn by Gagnier and Wilson (1996, Fig. 7G, H) are correct. Generally, the denticles point anteriorly, towards the opening of the mouth.

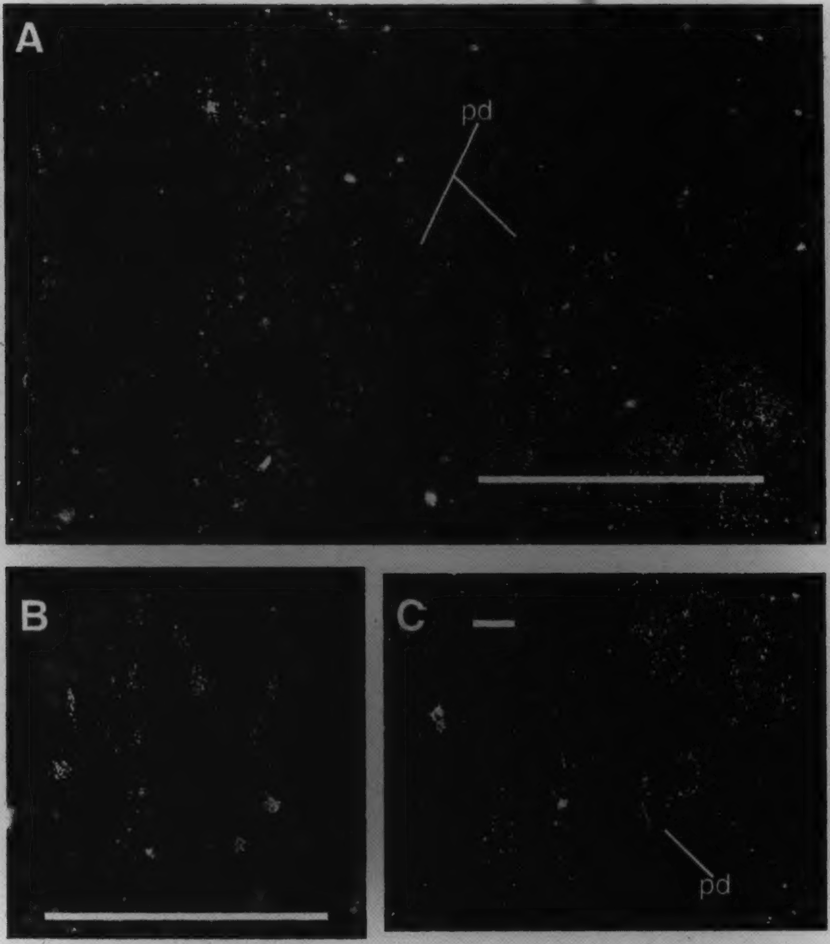

FIGURE 3.26. *Brochoadmones milesi* (UALVP 32406). **A**, rows of leaf-shaped pharyngo-denticles from below the otic sands; **B**, close-up of branchial denticle; **C**, pharyngeal denticles in basal and crown view. Scale bar for **A** equals 1mm, all other scale bars equal 0.5mm.

In a few of the specimens, there are some plates that, in crown view, appear to bear similar leaf-shaped denticles. The plates are sub-rounded in basal view and have clusters of the denticles. There is no clear pattern of the denticles on the plates, and they are not lined up neatly, as they are in UALVP 32406 (Fig. 3.26A). These plates begin in the rostral area, probably in the roof of the mouth, and their distribution extends into the branchial cavity.

It is possible that the branchial denticles are spread throughout the oral region and may be attached via different methods (some to plates and some organized into rows). These are probably specialized, modified tooth whorls, similar in function to the stellate plates discussed in the putative chondrichthyans.

Order ISCHNACANTHIFORMES Berg, 1940

Family ISCHNACANTHIDAE Woodward. 1891

Genus *ISCHNACANTHUS* Powrie, 1864

(Fig. 3.27-3.29)

Diagnosis—This is a diagnosis of the tooth whorls and associated structures of the genus. For more complete morphological and individual species diagnoses, see Hermus (2003) and Hanke (2001:339-360). Tooth whorls with pointed rows of teeth; teeth in one medial row and at least 2 lateral rows; base thin, recurved in semi-circle; whorls usually in rostral area, separated from dentigerous jaw bones of the same individual; whorls similar in morphology to rostral scales (see Chapter 4), but larger and more complex.

Material—Isolated tooth whorls: UALVP 41663, 42055, 42661, 45087, 47223; tooth whorls associated with body specimens: UALVP 19261, 19267, 32405, 32470, 32520, 39058, 39060, 39086, 42201, 42202, 42520, 42659, 42664, 44027, 45039, 45097, 45548, 47113.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—The tooth whorls of various species within the Ischnacanthidae have been described many times, but very rarely in detail. Gross (1971) is among the few to have done a detailed morphological and histological analysis of the tooth whorls of acanthodians, and not much has been published since.

For this study, instead of describing the tooth whorls of the different species of *Ischnacanthus*, I will give an overall description of the whorls seen within the genus. The whorls within the various taxa all have, overall, a very similar morphology and their structure and growth is almost the same among all of the species. For specific species descriptions, a more detailed study will need to be done. Like the tooth whorls discussed for *B. milesi* (see above description), the tooth whorls of *Ischnacanthus* spp. are generally smaller in relation to body size than the tooth whorls seen in the previously discussed putative chondrichthyans.

The tooth whorls are found at the anterior region of the oral cavity, anterior to the dentigerous jaw bones, and were possibly attached to the cartilages in both the upper and lower positions. Each tooth whorl consists of a thin recurved base bearing several rows of teeth. The whorls vary in size and number, and are not always present, or found in situ in all of the specimens. I believe this is in part because the tooth whorls are not firmly attached to any mineralized tissue, unlike the teeth to the dentigerous jaw bones, and were among the first things to become disassociated from the body during preservation (Figs. 3.27, 3.28, 3.29).

Tooth Crowns—The tooth crowns are always smooth and conical. Some species of *Ischnacanthus* have primary cutting edges along the lateral edges of the crowns. These cutting edges follow the curvature of the tooth. The cutting edges are best seen in the larger teeth, but appear to be present in all of the teeth of the whorls where preservation is sufficient. There is no evidence for secondary cutting edges, but to be certain of this, some of the tooth whorls should be removed from a specimen, further prepared and analyzed using the SEM.

There are usually three to five rows of teeth, with the central, medial row having the largest teeth. These large teeth are slightly recurved and directed lingually, into the oral cavity. The largest tooth is found in the most lingual position (Fig. 3.27D, 3.28, 3.29B).

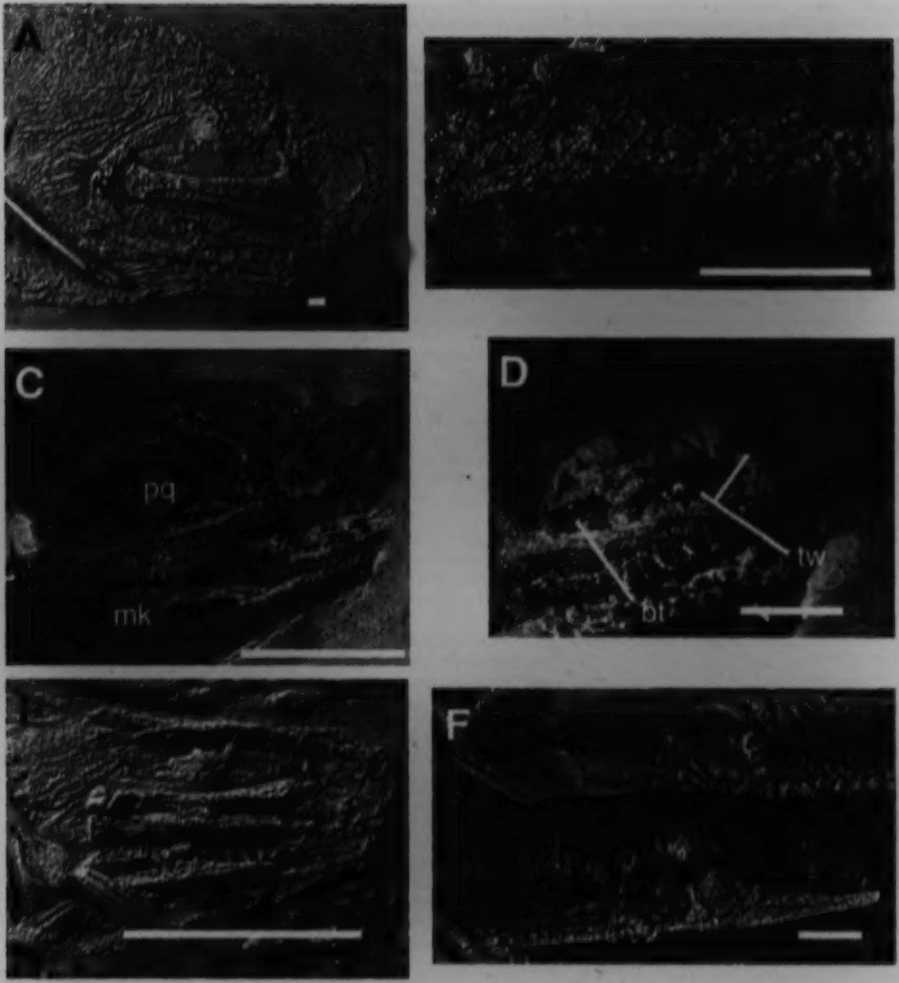

FIGURE 3.27. *Ischnacanthus* sp. **A-B**, UALVP 45014, **C-D**, UALVP 42201, **E-F**, UALVP 32405. **A**, head of *Ischnacanthus* sp. with assorted dentitions; **B**, basibranchial teeth; **C**, head of *Ischnacanthus* sp. with dentigerous jaw bones and cartilages, labial scales and displaced tooth whorls; **D**, close-up view of the displaced tooth whorls of various size; **E**, head of *Ischnacanthus* sp. with dentigerous jaw bones, labial scales, tooth whorls and basibranchial teeth; **F**, close-up of a displaced tooth whorl and two basibranchial teeth. Scale bar for **C** equals 0.5cm, for **E** equals 1cm, all other scale bars equal 1mm.

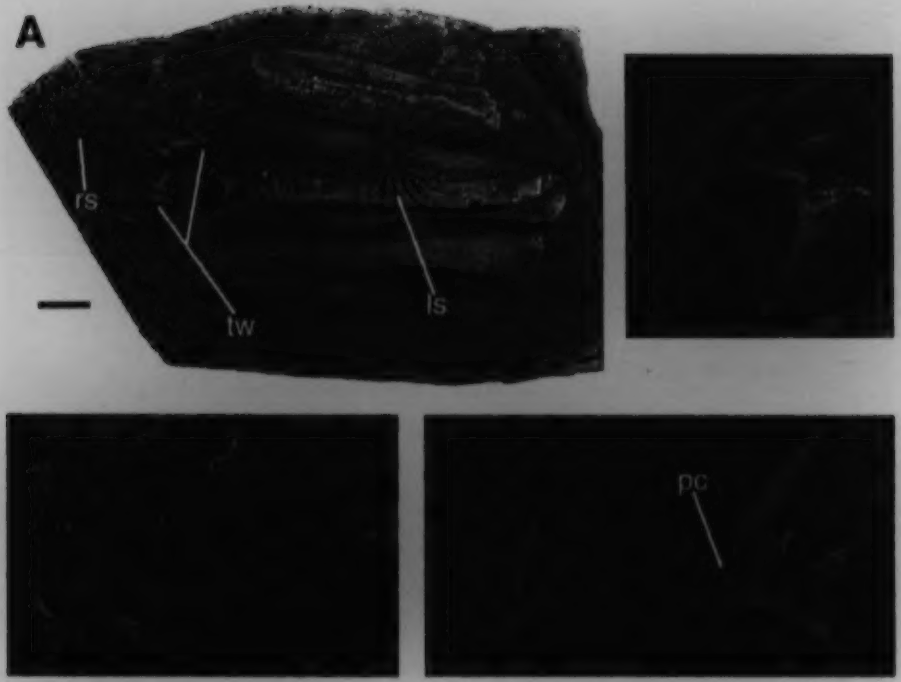

FIGURE 3.28. *Ischnacanthus* sp. (UALVP 32520). **A**, four dentigerous jaw bones with tooth whorls, labial scales and rostral scales; **B**, recurved tooth whorl from the lower jaw; **C**, two tooth whorls from the upper jaw with some rostral scales; **D**, two tooth whorls from the lower jaw. Scale bar for **A** equals 1mm, all other scale bars equal 300um.

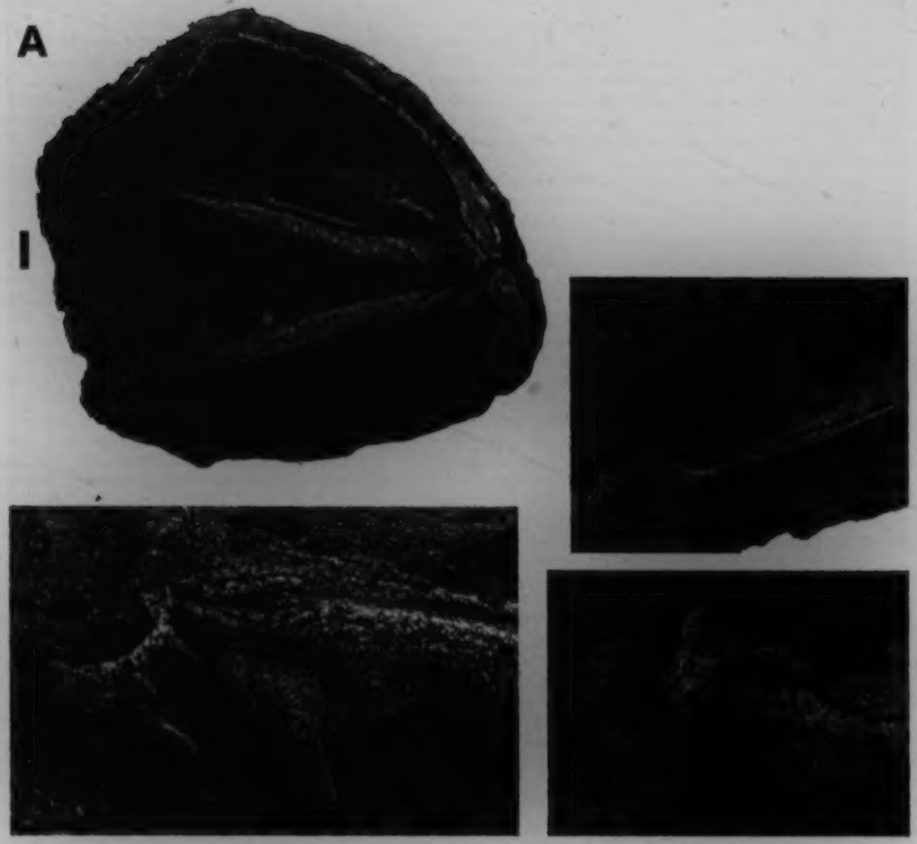

FIGURE 3.29. *Ischnacanthus* sp. (UALVP 47223). **A**, articulated upper and lower left dentigerous jaw bones and cartilages with symphyseal tooth whorls; **B**, upper tooth whorl, embedded? in the cartilage; **C**, lower tooth whorl on the edge of the jaw bone; **D**, close-up of the lower tooth whorl. Scale bar for **A** equals 1mm, all other scale bars equal 300um.

The number of lateral rows of teeth varies among the species of *Ischnacanthus*, but the number of right and left lateral rows on each whorl are equal. The teeth in the lateral rows are much smaller than the teeth in the medial row. The lateral teeth are also pointed and conical, with no ornamentation or cutting edges. The lateral teeth are otherwise identical in morphology to the medial teeth (Fig. 3.28).

Like the medial row, the teeth increase in size lingually and the lateral rows are continuous along the entire base of the tooth whorl. All of the teeth in the lateral rows are in line with the corresponding tooth in the central row. The teeth are all equally spaced and do not become more closely packed as the larger teeth are added (3.27B, 3.28).

Base—The bases of the tooth whorls of *Ischnacanthus* are very thin and recurved. Some of the larger tooth whorls have a base recurved like a semi-circle, while others can be completely recurved on themselves (Fig. 3.28, 3.29).

The bases appear to widen slightly lingually, to accommodate the larger teeth. The thickness of the base in all of the tooth whorls is consistent throughout the length of the whorl. In basal view, the base is smooth and does not show any obvious evidence of vascular canals. There is no evidence for these canals on the side of the base either (Fig. 3.28).

Attachment of the Teeth—Due to the small size and delicate detail of the tooth whorls of *Ischnacanthus* spp., it was not possible for me to remove any of the tooth whorls for further preparation to understand better how the teeth are attached to the base. The teeth are generally firmly attached to the base of the whorl and do not show a clear zone of attachment like that seen in the putative chondrichthyan condition.

There are some tooth whorls with teeth that are not as firmly attached to their base. They appear to be detached from the base along a continuous line (Fig. 3.28D). There is no evidence for finger-like projections or any vascular canals along this line. It is possible that the separation is an artifact of preservation, along a weaker part of the tooth whorl rather than a true attachment area. For a better understanding of the attachment of the teeth, some of the tooth whorls should be removed, prepared, imaged by SEM, and if they are large and thick enough, thin-sectioned for histological information.

Internal Structure—The teeth on the tooth whorls are hollow, with a hollow pulp cavity extending the entire length of the tooth crown. This is typical of ischnacanthid tooth whorls, and is what was seen here in broken teeth (Fig. 3.28D).

Basibranchial Teeth—In multiple specimens of *Ischnacanthus*, there are single teeth associated with the oral cavity. These teeth are thin, long and needle-like. They have a single crown, and an open pulp cavity, with a circular base (Fig. 3.28).

They are very widely spaced in a line below the Meckel's cartilages and do not seem to be associated with the dentigerous jaw bones or the tooth whorls. They are not found in paired groups. Because of this, these teeth are most likely associated with the basibranchial cartilage found medio-ventrally in the oral cavity.

In at least one specimen of *Ischnacanthus*, one can see these single needle-like teeth in the basibranchial position, but also others in the upper region of the oral cavity. It is unlikely that these teeth are displaced because there is more than one of them in this region, and they are similarly spaced to those in the basibranchial position. These teeth are also unpaired and are most likely found in a single row.

Cartilage does not ossify readily (Carroll, 1988) and is not usually preserved during fossilization. The inferred positions of the isolated teeth are based on relative positions of the teeth on the oral cavity as well as reconstructions of the cartilages in *Acanthodes* (Denison, 1979).

Remarks—These teeth are similar to structures referred to as 'gill rakers' in *Homalacanthus connicus* (Gagnier, 1996). Gagnier believed that these teeth were gill rakers lining the gill arches and are only found associated with the jaw cartilages due to secondary displacement after death. I believe that it is very possible that these teeth are similar to the basibranchial teeth seen in *Ischnacanthus* based on their similarities in morphology and positions in the oral cavity.

The function of these teeth is unclear; they are delicate and widely spaced from each other, making them unlikely to aid in the predatory habits of these fish. It is possible that these may have had a similar function to placoid scales in the bucco-pharyngeal area of sharks (Raschi and Tabit, 1992); to help process food farther into the mouth, or to help keep it from escaping back out of the gape.

DISCUSSION

Overall, the tooth whorls in the various species of Eugnathostomata from the MOTH locality consist of one or more rows of teeth along a recurved base (the degree of recurvature varies greatly within and among taxa). In all of the tooth whorls discussed, I feel confident in comparing tooth whorls to tooh families in sharks. These similarities are in how the teeth grew and were added and moved through the mouth, as discussed by Williams (2001). However, there are clear morphological and histological differences between the tooth whorls of acanthodians and putative chondrichthyans, supporting their provisional assignment to different higher taxa.

In addition to a variation in the morphology and histology of the tooth whorls in the Eugnathostomata from MOTH, there is also an assortment of teeth and tooth-like structures associated with the tooth whorls in these different taxa. These associated tooth types also vary greatly within and between taxa, but do show some similarities and differences between the two groups.

In none of the tooth whorls in this study is there evidence for shedding of the complete whorl in the mouth. If this did occur, it would be expected that there would be a newly formed whorl or, at least, a single tooth to replace it. This is also unlikely to occur because of the similarities all of the tooth whorls share with tooth families seen in sharks, which do not lose and replace tooth families.

Putative Chondrichthyan Tooth Whorls

As mentioned in the above chapter, many of the tooth whorls discussed were isolated and not found with any associated body materials. Much of the association of these tooth whorls to the Chondrichthyes is the similarity of these tooth whorls to the tooth whorls belonging to more completely preserved putative chondrichthyans such as Gen. Nov. B et sp. nov. A. These morphological characteristics are discussed below.

The tooth whorls seen in putative chondrichthyans are larger and more robust than those seen within the Acanthodii. These whorls are usually found lining the upper and lower jaw margins and in some cases they are also seen to transform into other similar, associated types of dentition within the mouth and throat.

The teeth can be arranged either in a single row or in multiple rows in younger whorls, transforming to a single row in older whorls. These tooth whorls are made up of teeth with primary and usually secondary cutting edges along their medial edges.

The putative chondrichthyan tooth whorls grew via the addition of new teeth to the lingual side of the whorl. From morphological and histological data it is apparent that the teeth are added to the whorl before the underlying supporting base is completed

The teeth are attached to the base via finger-like projections extending from the bottom of the teeth into the base and seem to attach to the linguo-most part of the whorl last. The teeth grow piggy-backed onto one another and become more fused to the base as they become older. This type of tooth addition/growth is similar to what was described by Gross (1971) in the tooth whorls of the acanthodians *Gomphonchus* and *Nostolepis striata.*

This type of growth was seen in all of the species, with the exception of Gen. Nov. C sp. cf. sp. nov. A. In this species, the teeth were lost at some point before preservation. It is doubtful that these teeth were lost during the life of the animal. It is more likely that the teeth were loosely attached to the bony base, and when the animal died, the teeth were lost or shed from the whorl, also explaining the presence of the shed teeth scattered on the same block with the whorls.

The bases are thick and heavily vascularized by means of canals that can be traced throughout the base and into the tooth crowns. The bases increase in thickness and width as the younger, larger teeth are added.

The individual teeth vary greatly in external morphology but all have an internal histology of a network of canals instead of a single pulp cavity. This condition is referred to as the anaulacorhize stage of osteodont histology (Cappetta, 1987). The degree of the networking of the canals varies among the different species of putative chondrichthyans, but they all exhibit this histology to a certain extent.

Acanthodian Tooth Whorls

Acanthodian tooth whorls are smaller and more delicate in appearance than those of putative chondrichthyans. They are found aligned on the upper and lower jaw margins, as in *Brochoadmones milesi*, or in a symphyseal or parasymphyseal position, as in *Ischnacanthus* spp.

The teeth are arranged in multiple continuous rows or in multiple rows initially, transforming into a single row of teeth as the whole whorl ages. The teeth are usually long and conical and are directed into the oral cavity. They are smooth and rarely have cutting edges; if cutting edges are present, there are only primary ones and no secondary cutting edges.

The teeth are not as tightly packed together as they are in the tooth whorls of putative chondrichthyans. The pattern of addition of the teeth in acanthodian tooth whorls is unclear. There is no evidence of piggy-back attachment like that seen in the putative chondrichthyans. It does appear in some of the specimens that the base of the tooth whorl grew before the youngest tooth was added. The small-scale CT-scanner was not of high enough resolution to give useful histological information. Further studies and thin-sections need to be done to clarify this.

The teeth of the examined acanthodian whorls all have a single, hollow pulp cavity. This condition is referred to as the holaulacorhize stage of osteodont histology (Cappetta, 1987), and is similar to what was seen in the dentigerous bony plates of *Ischnacanthus* spp. dentigerous bony plates (see Chapter II).

The bases are thin and show no obvious evidence of vascularization. They do not increase in thickness, only increasing in width to accommodate the younger, larger teeth.

Little is known about the detailed histology of these acanthodian tooth whorls because all of the specimens from the MOTH collection are too small to thin-section. In the future, it would be useful to identify some larger acanthodian tooth whorls, thin section them and compare their histologies to what was described by Gross (1971) and Ørvig (1973).

Ontogenetic Change of Tooth Whorls

We see ontogenetic change within several of the tooth whorls from the MOTH locality. In all the tooth whorls used in this study, there is a clear pattern whereby the teeth become larger and more robust as they get younger (as the fish becomes older). There appear to be at least two different types of tooth whorl change seen in the Eugnathostomata: (1) change of tooth morphology, and (2) change in number of rows of teeth.

Change in tooth crown morphology is illustrated in Gen. Nov. D et sp. nov. A. This species shows clear transformations from small and rounded, to V-shaped with a keel, to long and pointed between the youngest and oldest teeth. Although this is the best example of ontogenetic change in a single tooth whorl, a similar pattern is seen in both the putative chondrichthyans and acanthodians in this study.

A change in tooth number is clearly seen in the putative chondrichthyan Gen. Nov. B et sp. nov. A, as well as in the acanthodian *Brochoadmones milesi*. In both of these species, the tooth whorls transform from multiple rows of older, tightly packed, smaller teeth to a single row of younger, more pointed teeth. As this is seen in multiple members of the Eugnathostomata at MOTH, it is likely this reflects a common ontogenetic pattern and is not a specialization characteristic of a certain type of tooth whorl or a particular clade.

In all of the cases, the change in tooth morphology and number is most likely due to a shift in life history during ontogeny. Most probably a change in diet, such as a transition from a scavenging or microphagous lifestyle to a more macrophagous, predaceous one, was involved. As mentioned in the dentigerous jaw bone section of this thesis (see Chapter II), there would have been a transitional stage for the animal where the change in tooth types would allow for a varied diet, both micro- and macrophageous, before the adult form was attained. More work needs to be done on this subject before any firm conclusions can be drawn. It would be interesting, for example, if stomach contents could be analyzed in younger and older individuals of a single species.

Associated Tooth Types

In many of the specimens that have tooth whorls, there have been observed additional associated tooth types. Although these associated teeth vary considerably among the taxa, in all cases, similarities can be drawn between the tooth whorls in question and the associated tooth types. In the future this could allow association of whorls with other dental elements of the same species in acid-dissolution residues and other similar situations.

The isolated basibranchial teeth seen in *Ischnacanthus* are no doubt true teeth, although their function still remains unknown. It is unlikely that they aided directly in the catching and processing of food because of their wide spacing and delicate construction but they may have somehow prevented food from escaping the mouth once engulfed. It is evident that these teeth were not replacement or new teeth that were being added to the dentigerous bony plates or the tooth whorls as their morphologies all differ greatly from those elements.

The pharyngo-denticles seen in *Brochoadmones milesi* grow and are organized in a very similar way to the tooth whorls of the same species. It is likely that these are modified teeth that may have migrated farther back into the oral cavity and become specialized.

It should be noted that there is a difference between the morphology and organization of the tooth whorls and that of the remainder of the dentitions in Gen. Nov. B et sp. nov. A and Gen. Nov. B et sp. nov. B. The tooth whorls consist of multiple rows of teeth that have become fused together. The stellate plates, although similar in basal view to the tooth whorls, are much less organized and are more reminiscent of the tesserae of osteostracans (Hawthorn et al., in press). The mosaic and rosette plates of Gen. Nov. B et sp. nov. A are organized in a very scale-like pattern and are not a very tooth-like part of the dentition of this animal. This is an example that supports the idea that teeth and tooth whorls may have come from a modified scales or denticles in the oral cavity.

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IV. TOOTH-LIKE LIP SCALES OF THE EUGNATHOSTOMATA FROM THE LOCHKOVIAN (EARLY DEVONIAN) MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA

INTRODUCTION

Hypotheses for the Origins of Teeth

The evolutionary origin of teeth is a heavily studied topic for which there are two main hypotheses. The first is that they evolved from denticles lining the oro-pharyngeal cavity of early, jawless vertebrates (e.g., Smith and Johanson, 2003). The second hypothesis is that the scales on the head near the mouth became specialized for grasping food, migrated into the mouth and became teeth (Hertwig, 1874). There is currently no consensus as to which of these two hypotheses is correct, and an important line of evidence will be possible intermediate conditions seen in the fossil record.

The hypothesis that teeth evolved from denticles lining the oro-pharyngeal cavity has been supported by the discovery of whorl-like denticulated platelets in thelodonts such as *Loganellia* (Smith and Coates, 2000), but is weakened by the absence of comparable structures in other agnathans, including osteostracans, which are often considered to be the sister group of gnathostomes (Donoghue and Sansom, 2002).

The idea that teeth evolved from scales is not a new one. Hertwig (1874) originated the concept of a homology between the placoid scales of sharks and teeth in vertebrates. He argued that placoid scales were very tooth-like and believed that scales migrated into the mouth and were secondarily adapted to capture and process food.

Tooth Precursors from the MOTH Locality

In this chapter, I will focus on examples of possible tooth precursors, in the form of specialized labial and rostral scales fringing the "lips" of certain representatives of the Eugnathostomata (see Chapter I) from the Lochkovian MOTH locality in northwestern Canada. I will be looking at one example within the putative Chondrichthyes and one within the Acanthodii, which will allow for a limited comparison of labial scales between the two groups.

In both cases discussed below, the elements being studied are clearly scales and not true teeth, as a complete series of transitional forms from typical head scales to specialized lip and/or rostral scales can be seen on the external surface of the heads of the fossils.

Detailed information about locality, materials and methods is found in Chapter I.

Institutional and Locality Abbreviations—MOTH, Man On The Hill locality, northwest Territories, Canada; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton.

Anatomical Abbreviations—fs, fan-shaped scales; **hs,** head scale; **l,** left; **lbp,** lower bony plate; **ls,** labial scale; **r,** right; **rs,** rostral scale; **sc,** stomach contents; **tw,** tooth whorl; **ubp,** upper bony plate.

SYSTEMATIC PALEONTOLOGY

Superclass GNATHOSTOMATA

EUGNATHOSTOMATA DeIuliis and Pulera, 2007

Class CHONDRICHTHYES Huxley, 1880

Order incertae sedis

Family incertae sedis

Genus *OBTUSACANTHUS* Hanke and Wilson, 2004

OBTUSACANTHUS CORROCONIS Hanke and Wilson, 2004

(Fig. 4.1-4.2)

Revised Diagnosis—This is a diagnosis for the head/mouth region and associated structures of *Obtusacanthus corroconis*. For a complete diagnosis, see Hanke and Wilson (2004:196). Putative chondrichthyan with mouth large; palatoquadrate and Meckel's cartilages not calcified; marginal jaw teeth and other dentition absent; head scales round, stellate, transforming near the mouth to labial scales; labial scales pointed, with elongate crowns directed towards the mouth gape.

Holotype—UALVP 41488.

Material—UALVP 19338.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—Although the UALVP collection has several specimens of *Obtusacanthus corroconis*, only the holotype, UALVP 41488 (Fig. 4.1A), is preserved laterally compressed, with the head still intact. Fortunately, this specimen is beautifully preserved, and nearly complete. This provides us with great detail of the morphology of the mouth and surrounding scales. *Obstusacanthus corroconis* is a small putative chondrichthyan with no preserved cartilage, bony plates or teeth, but it does possess small fin spines, as well as scales covering the body and head, and specialized labial scales located in the skin along the upper and lower margins of the mouth. There is no evidence of a calcified palatoquadrate or Meckel's cartilages in any of the specimens and there are no teeth or tooth whorls where the cartilages would have been in life.

Labial Scales—The labial scales of *O. corroconis* are arranged in the skin adjacent to the upper and lower margins of the mouth opening, and transform from the typical head scales (Fig. 4.1B) closest to them. The typical head scales

FIGURE 4.1. UALVP 41488, the holotype and only complete specimen of *Obtusacanthus corroconis*. **A**, full body of *O. corroconis*, preserved in right lateral view; **B**, close-up of the gape, note the rapid transistion from head tolabial scales; **C**, a close-up of the labial scales, note how they are pointed into the mouth. Scale bar for **A** equals, all other scale bars equal 1mm.

are rounded and almost symmetrical, with stellate ornament in the form of five to seven radiating ridges as well as branching ridges coming off the main ridges.

The transformation from head to labial scales occurs over a short distance, the labial scales becoming more elongated and more pointed closer to the mouth margin. Usually there is just a single row of fan-shaped, transitional scales (Fig. 4.1B) between typical head scales and more pointed labial scales.

The fan-shaped, transitional scales are asymmetrical, with the points facing towards the opening of the mouth. The center of radiation for the ridges on the scales is closer to the side of the scale near the mouth, and it now holds only four to five branches with smaller branches coming off the main ones, forming a wide V-shape or fan-shape.

The labial scales are elongate with three to four main ridges. When comparing these scales to the regular head scales, it appears as if the center of radiation were drawn out to a point, forming the tip of the scale crown. The ridges, although reduced in number, still radiate from the center but are now taller and thinner when compared to those of the head scales (Fig. 4.1C).

The labial scales are directed toward the mouth, suggesting that they may have been useful for grasping food and perhaps helping move it into the gape. Scales near the angle of the jaws are not modified into lip scales. Modified lip scales occur from the front to a point a little farther back than two-thirds of the way to the angle of the gape. Posteriorly, these specialized scales are only a single row wide. Progressively more anteriorly along the lips, the number of rows of these specialized, labial scales increases. At the front of the mouth, beneath the rostrum, there are fours rows of labial scales.

Stomach Contents—It is evident, in at least two specimens, that although *Obtsacanthus corroconis* had no teeth or other recognizable forms of dentition, they were predatory. In the holotype, UALVP 41488, remains of gut contents are preserved in what appears to have been a full stomach (Fig. 4.1A). Due to the excellent preservation of this specimen, the stomach is still fully covered in scales, preventing identification of what it may have eaten.

UALVP 19338 (Fig. 4.2) is a much more poorly preserved specimen of *Obtusacanthus corroconis*, showing little of the body besides dorsal and pectoral spines, and some scattered patches of scales, which allowed the identification of the specimen to species. The only other part that was preserved is the partially digested gut contents. I can be sure that they are stomach contents because there are some *O. corroconis* scales both above and below the material in question. Upon closer inspection, I have concluded that the bits belong to an unidentified cephalaspid as well as a *Lepidaspis*-like osteostracan.

Remarks—From the above descriptions and close specimen observation, it is clear that *Obtusacanthus corroconis* had the ability to be a predator or scavenger of some sort. Although it does not have true teeth of any kind, the labial scales are very tooth-like in appearance and may have served as an analogous structure with a similar function to teeth. Based on their morphology, it is much more likely that the labial scales would have been used to aid in

FIGURE 4.2. *Obtusacanthus corroconis* (UALVP19338). Specimen with fossilized gut contents identified as bits of *Lepidaspis*-like (heterostracan) bone and cephalaspid bone. Scale bar equals 1cm.

grasping and engulfing prey rather than that they would have been used for tearing or ripping off pieces of flesh. The pieces of heterostracan and osteostracan bone in the gut of UALVP 19338 show that at least this animal was preying or scavenging on multiple species and was able to engulf and swallow small parts of them.

Class ACANTHODII Owen, 1846

Order ISCHNACANTHIFORMES Berg, 1940

Family ISCHNACANTHIDAE Woodward. 1891

Genus *ISCHNACANTHUS* Powrie, 1864

(Figs. 4.3-4.4)

Revised Diagnosis—This diagnosis is limited to specialized rostral and labial scales; for a detailed diagnosis of additional dentitions, see Chapters II and III in this thesis; for full species diagnosis, see Hermus (2003). Acanthodians with dentigerous bony plates, tooth whorls, specialized tooth-like labial and rostral scales; labial scales multicuspid, elongate, formed in skin external to upper and lower dentigerous bony plates; labial scales arranged in curved, whorl-like rows focused on a point two–thirds of the length of the gape from the front of the mouth; rostral scales multicuspid, tooth whorl-like, extending from the head onto the rostrum; rostral scales intermixed with larger tooth whorls at internal margin of mouth.

Material—19267, 32405, 32414, 32470, 32520, 39063, 39086, 41491, 41920, 42201, 42659, 42660, 42664, 44027, 45014, 45034, 45035, 45039, 45082, 45087, 45548, 45553, 47094, 47216.

Locality and Age—MOTH (Man On The Hill) locality, Mackenzie Mountains, Northwest Territories, Canada; Lochkovian (Early Devonian); Delorme Group.

Revisions to the Description—As described in previous chapters, species in the genus *Ischnacanthus* have many different types of teeth, including dentigerous bony plates, tooth whorls and other isolated teeth in the pharynx. In addition to these various types of teeth, *Ischnacanthus* spp. also have tooth-like labial and rostral scales (Fig. 4.3).

Hermus (2003) found that there were many different species of *Ischnacanthus* in collections from the MOTH locality, that they could be identified solely by different morphologies of their dentigerous bony plates, and that the body forms and scale coverings of the various species were identical. This is true of all of the specimens I studied as well, but I found that the labial and rostral scales vary as much as the morphologies of the dentigerous bony plates do between the different species. For this study, I focus on the general pattern and morphology of these specialized scales as seen in the genus *Ischnacanthus*, instead of attempting to describe different morphologies between species.

Labial Scales—The labial scales of *Ischnacanthus* spp. are not always preserved and, if the dentigerous bony plates have been disturbed during the

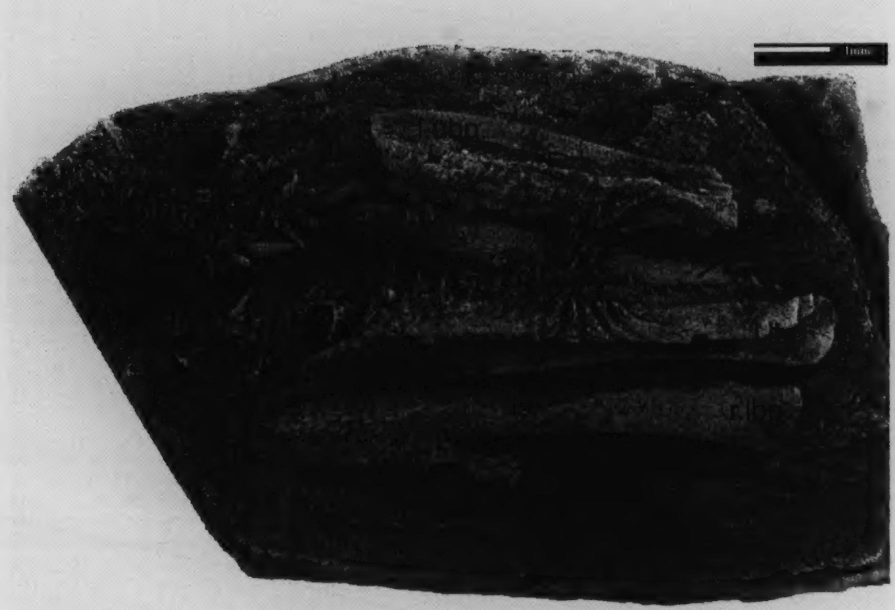

FIGURE 4.3. UALVP 32520, *Ischnacanthus* sp. Isolated elements of dentition. Anterior is to the left. Scale bar equals 1mm.

fossilization process, these scales are generally lost. They cover the upper and lower lips of the fish, and are usually organized in subparallel, curving, converging rows.

The individual scales are elongate, compound structures with a single row of cusps or several rows; each labial scale looks somewhat like a small tooth whorl that has been stretched out and flattened (Fig. 4.4A). The middle row of cusps is the largest, and the largest cusp on each labial scale is found in that row that is closest to the labial margin. Cusps decrease in size progressively with greater distance from the cleft of the mouth.

The scales generally point toward the cleft of the mouth and, in the laterally compressed fossils, they overly the dentigerous bony plates. At a certain point between half and two-thirds of the way from the anterior end of the dentigerous bony plates, the labial scales are the most highly developed. In this area, the density of labial scales is highest and their orientations are focused toward a point in the cleft of the mouth. This is seen on both the upper and lower labial scales of *Ischnacanthus* sp. (Fig. 4.3).

Rostral Scales—The rostral scales are found extending from the top of the rostrum, down to the underside of the rostrum and, in the compressed fossils, are found to be surrounding the upper tooth whorls described in Chapter III (Fig. 4.3, 4.4C), although the rostral scales were originally external and the tooth whorls were located internally in the mouth. It is unclear if such scales are also found at the front of the lower jaw, where they would be preserved surrounding

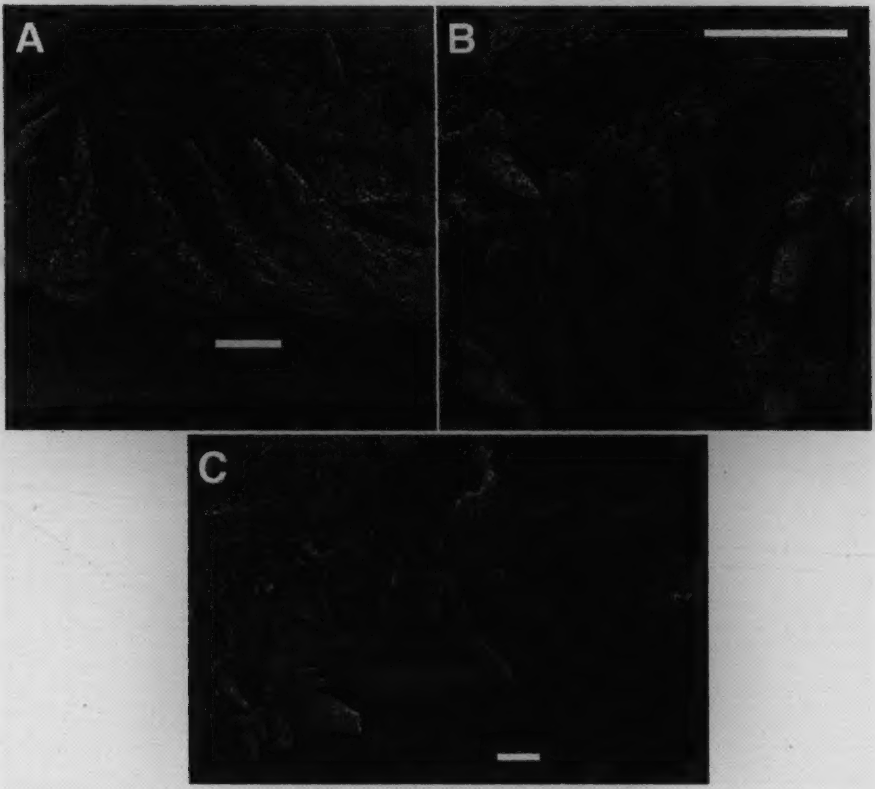

FIGURE 4.4. UALVP 32520, *Ischnacanthus* sp. **A**, close-up of the pointed rows of labial scales lining the left lower bony plate; **B**, close-up of the rostral scales; **C**, two upper tooth whorls, note the similarities in morphology between the tooth whorls, labial, and rostal scales (not taking size into account). Scale bars equal 200um.

the lower parasymphyseal tooth whorls. The rostral scales are usually similar in morphology to the labial scales, except that they are found on a recurved base, more like the shape of the actual tooth whorls (Fig. 4.4B). The cusps of each rostral scale are hollow and also resemble those seen in the tooth whorls.

The rostral scales are best developed on the underside of the rostrum. In all of the rostral scales, the largest cusp is found posteriorly on the scale, usually pointing into the mouth; this is a very similar morphology to that seen in the tooth whorls themselves.

Remarks—It is clear from this study that *Ischnacanthus* spp. at the MOTH locality possess an assortment of tooth-like labial and rostral scales. It is unclear what the exact function of these scales was. Perhaps they aided somehow in grasping food, or in keeping prey from escaping the jaws.

Ischnacanthus is not the only genus within the Ischnacanthiformes that has been reported as having tooth-like scales covering parts of the dentigerous bony plates. In his description of *Poracanthodes menneri*, Valiukevičius (1992) noted that there were tooth-like denticles covering the upper part and side of the mesial ridge of the bony plates. *Poracanthodes menneri* is another ischnacanthiform with a large assortment of teeth and tooth-like structures (dentigerous bony plates, tooth whorls) and associated tooth-like denticles. These denticles appear to have a similar morphology to those seen in *Ischnacanthus* spp., and most likely served a similar function.

To understand better the taxonomic distribution of these rostral and labial scales, more genera and species of Ischnacanthiformes should be closely analyzed to see if they also have similar structures. The more specimens that are found to have these interesting structures, the more morphological and paleoecological correlates could be gathered to allow formulation of functional explanations for these specialized, tooth-like scales.

DISCUSSION

Although many eugnathostomes had already evolved teeth by the time that the MOTH deposit was formed, the putative chondrichthyan *Obtusacanthus corroconis* did not possess them. It is possible that *O. corroconis* evolved its specialized labial scales as a functional analogue to the teeth seen in some of the other taxa at the time.

In the case of *Ischnacanthus,* the labial and rostral scales resemble the larger tooth whorls seen in the same species. In both, the scales appear to be grouped together in families or rows of cusps that are larger toward the margin of the mouth. These scales are different in appearance from the proposed 'tooth whorls' seen in thelodonts such as *Loganellia scotica* (Smith and Coates, 2000). The internal denticulated platelets of *Loganellia* are composed of denticles all of the same size; they do not increase in size like the tooth-like parts of the labial scales in *Ischnacanthus*. It is possible that the internal denticles in the thelodonts functioned as gill rakers do in jawed vertebrates, but this does not make them a good example of ancestral teeth as has been suggested by Smith and Coates (2000). Indeed, the tooth-whorl like rostal and labial scales of *Ischnacanthus* is a seen in the present study are arguably a much better model for the origin of teeth, but in this case from specialized head scales rather than from internal denticles.

From this study of one putative chondrichthyan (*Obtusacanthus corroconis*) and one genus of acanthodian (*Ischnacanthus* spp.), it is clear that at least some of the early members of the Eugnathostomata possessed specialized labial scales that illustrate possible developmental mechanisms and suggest possible pathways for the origin of teeth and tooth-like structures as modified scales. These taxa, however, occur with others that have well-developed teeth, and considerably after the first appearance of undoubted teeth in the fossil record of gnathostomes (e.g., in Silurian ischnacanthid and climatiiform acanthodians; Denison 1976, Janvier 1996).

Although the exact function of labial scales is unclear, as is how much they aided in feeding if at all, they nevertheless provide examples of early gnathostomes that possessed tooth-like scales along or near the 'lips' or mouth cleft. Because of this, they thus support the hypothesis that teeth could have originated from modifications of external scales (Hertwig, 1874), rather than necessarily from internal denticles (Smith and Johanson, 2003), by proving that such a transition was developmentally and evolutionarily possible.

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V. GENERAL DISCUSSION

Overview of Dentitions of MOTH Eugnathostomata

As discussed in the previous chapters, the dentitions seen in the MOTH eugnathostome fossil assemblage are very diverse and vary from labial and rostral tooth-like scales, to tooth whorls, to calcified and ossified jaws (some with dentigerous bony plates), to isolated teeth and denticles in the various parts (pharyngeal, branchial) of the oral and pharyngeal cavities.

It is not uncommon for acanthodians or putative chondrichthyans to have more than one of these types of teeth in the dentition. *Brochoadmones milesi* and *Ischnacanthus* are examples of acanthodians with multiple types of teeth. *Brochoadmones milesi* has tooth whorls lining the upper and lower jaw margins, larger, parasymphyseal whorls in the upper and lower positions, and tooth whorl-shaped branchial denticles. *Ischnacanthus* spp. have tooth-whorl-like labial and rostral scales, parasymphyseal tooth whorls in the upper and lower positions, ossified upper and lower jaws with overlying dentigerous, dermal plates, and isolated basibranchial (and possibly other cartilage-supported) needle-like teeth.

The two species belonging to Gen. Nov. B are examples of putative chondrichthyans with varied dentitions. Gen. Nov. B et sp. nov. A has tooth whorls lining the upper and lower jaws, as well as an assortment of other dentitions in the oral cavity. There are snowflake-shaped stellate plates covering the roof and floor of the mouth, grading into rosette and then mosaic, fan-shaped plates in the pharyngeal region. Gen. Nov. B et sp. nov B has a similar dentition of tooth whorls lining the upper and lower jaws, with similar stellate plates, in this case with a more sun-shaped ornament, inside the mouth.

In all of the above examples, it is most likely that the different dentitions were developed to aid in feeding. Based on Reif's (1982) definition of a tooth, I am comfortable stating that the tooth whorls are similar to rows of teeth belonging to a tooth family, are arranged in rows with the replacement tooth already formed, and were probably developed within a dental lamina (obviously not preserved). This is similar also to the branchial denticles seen in *B. milesi*. The isolated basibranchial teeth in *Ischnacanthus* are also most likely teeth, based on their tooth-like morphologies and their similar arrangement in rows in multiple species and specimens.

It is not as clear to me if the associated dentitions (stellate, rosette, mosaic plates) seen in the two species of Gen. Nov. B are teeth or denticles. Although, in basal view, the stellate plates are very similar to the associated tooth whorls, there does not seem to be a clear pattern to their formation and development; they are all various sizes and seem to grow at least until they come into contact with one another. It seems likely that these would be considered denticles, much like what is seen in the tuberculated, bony armor of some placoderms (Young, 2003), or the external bony tesserae in some osteostracans (Hawthorn et al., in press).

It should also be noted that, in the specimens possessing dentigerous tooth plates and parasymphyseal tooth whorls (*Ischnacanthus* spp.), the individual teeth in the whorls did not change in morphology or number throughout ontogeny; the teeth just increased in size. In species where tooth whorls are lining the upper and lower jaw margins, the teeth tend to change throughout ontogeny, either in number or in morphology. This condition is similar to what is seen in the specimens with dentigerous bony plates (Ischnacanthidae, Tetanopsyridae) with the older teeth being smaller and less ornamented and the younger ones larger and more ornamented. This condition is possibly due to a change in diet and possible feeding habits throughout ontogeny.

In the specimens with ossified or calcified jaws (complete or partially) but without teeth, it is questionable if they are primitive or derived forms. The morphologies of these taxa (*Kathemacanthus*, *Gladiobranchus*, and *Tetanopsyrus breviacanthias*) differ greatly from one another and it is doubtful that they represent a common, primitive condition. If this is true, it would imply that these are three derived forms with jaws having reduced dentitions and calcification/ossification. This may support for the idea that the evolution of bony jaws and teeth are strongly associated.

Similarities to Dentitions in Other Devonian Eugnathostomata

As mentioned in the previous chapters, the assortments of dentitions seen in the fishes from MOTH are not unlike those of other acanthodians and chondrichthyans from the early Devonian, and also share some similarities with those of other members of the Eugnathostomata.

The preservation of tooth families, in tooth whorl form and in unfused forms, is seen in many acanthodians and chondrichthyans. In tooth whorl form they are seen in the acanthodians *Climatius reticulatus* (lining at least the lower jaw margin; Watson, 1937), and *Poracanthodes menneri* (in a symphyseal position in the lower jaw; Valiukevičius, 1992), and in the chondrichthyans *Helicoprion ferrieri* (Hay, 1909) and *Edestus leidy* (Hay, 1907). The teeth are seen in unfused tooth families in early chondrichthyans such as the cladodont shark *Ctenacanthus* and in cladoselachians (the used teeth are not shed, but retained for an unknown amount of time; Williams, 2001), and in the most primitive articulated chondrichthyan *Doliodus problematicus* (Miller et al., 2003) apart from the putative chondrichthyans of the present study. In acanthodians, it is possible that unfused tooth families are preserved as basibranchials and other similar dentitions like those seen in *Homalacanthus concinnus* (initially described as 'gill rakers'; Gagnier 1996).

Calcified and/or ossified jaws are also seen in many other forms of acanthodians and chondrichthyans. Ossified jaws with dentigerous bony plates are seen in the acanthodian *Poracanthodes menneri* (Valiukevičius, 1992). Partially ossified Meckel's cartilages are seen in the acanthodian *Diplacanthus striatus* (Watson, 1937). Calcified cartilages are seen in various chondrichthyans, including *Doliodus problematicus* (Miller et al., 2003).

When compared to actinopterygians, the dentitions mentioned above differ greatly. The teeth of *Cheirolepis canadensis* redescribed by Arratia and Cloutier

(1996) are numerous and diverse in morphology and location within the mouth. The teeth are socketed, monocuspid and conical in shape. Although the teeth are very different, there are similarities with taxa described in the present study in that there is an assortment of differing dentitions throughout the oral cavity. There is also evidence of smaller, unorganized teeth in association around the larger teeth. It may be that these teeth are actually denticles, similarly to what is seen in sharks (Nelson, 1970), the putative chondrichthyans in this study (see previous chapters), and placoderms (Young, 2003).

The teeth in sarcopterygians are similar to those seen in the actinopterygians in that they are socketed in the bones of the jaw and mouth, as well as being surrounded by smaller denticles (Zhu and Schultze, 1997; Andrews et al, 2006). One of the main differences is that many of the Devonian sarcopterygian fishes possessed single or paired tooth whorls in the lower symphysis. In at least one extremely well-preserved specimen of *Onychodus jandemarrai* (Andrews et al., 2006), the whorls are so well preserved in both juvenile and adult forms that it can be seen that these fish had a replacement pattern for the individual teeth, which were never fully fused to the base. It is unlikely that these tooth whorls are directly homologous to those discussed in detail in this study (see Chapter III), but they probably served a similar function.

The dentitions of lungfish are extremely derived and unique, and look like nothing else discovered in the fossil record. The separate teeth becoming fused onto tooth-bearing plates and later ankylosed to the supporting jaws (Kemp, 2002) may be similar in function to the tooth whorls discussed in Chapter III or to the dentigerous bony plates discussed in Chapter II, but it is unclear if they are directly homologous.

The question of true, homologous teeth in placoderms is still one of great debate. Due to the completely different jaw morphologies compared to the rest of the Gnathostomata (Carroll, 1988), it is unlikely that the teeth discussed here are homologous to those seen in the placoderms. This idea is reinforced by the fact that 'teeth' are only suspected in the highly derived forms of placoderms (Young, 2003; Johanson and Smith, 2005). This would imply that teeth evolved more than once, which is not very parsimonious, but possibly true.

In his odontode-regulation theory, Reif (1982) described the dentitions of various forms of gnathostomes. In this differentiation among the taxa, there was a commonality to them all, and although the morphologies, replacement patterns and functions may have differed greatly, they all originated in a dental lamina. This implies a common ancestor and a homology within the various structures. I believe this is also the case in the tooth-whorl-like dentitions of the specimens examined in this study.

Possible Implications

There is no evidence of a shedding or a tooth-replacement mechanism in any of the specimens possessing teeth, whether on tooth whorls, on dentigerous bony plates, or in the basibranchial teeth. This may support the theory proposed by Williams (2001) that tooth replacement is a derived condition only seen in more advanced/derived fishes. It may also imply that, although these three forms of dentition are morphologically very different, they may share a homologous source yet be functionally diverse because they are adapted to the lifestyle of the individual taxa.

The similarity between the dentigerous bony plates and tooth whorls is striking. It is also important to note that, in both cases, these structures are sitting above the palatoquadrate and Meckel's cartilages. Could it be that the teeth are producing the surrounding, supportive bone? If this is the case, it could be similar to alveolar bone, which has been proven to be formed by the teeth and not the supporting jaws (Ten Cate, 1970, 1971). This is completely hypothetical at this time but would be something to examine more closely in future thin-sectioning of the whorls and bony plates.

It is clear that there is no simple answer to the problem of understanding the evolutionary development of teeth. There does appear to be a large diversification of taxa with various forms of teeth and it is most likely that they are all derived from a single, primitive form. If these teeth were all derived from the placoid scales of sharks (Hertwig, 1874), it is not proven from the observations made in this study. However, from this study, there is evidence for both major models for the origin and development of teeth, namely that teeth evolved from specialized head scales (*Obtusacanthus corroconis*, *Ischnacanthus* spp.; see Chapter IV), or that they evolved from from oro-pharyngeal denticles (Gen. Nov. B et sp. nov. A; see Chapter III).

It is unclear which of these developmental models is correct because the eugnathostomes studied are already very derived and many forms possess true teeth. However, these results do demonstrate the existence of similar developmental patterning for tooth-like structures as required by both hypotheses. I am more inclined to believe the hypothesis that teeth developed from head scales due to the increased evidence as well as the similarities of the labial/rostral scales to the teeth and tooth whorls discussed in previous chapters. The specialized pharyngo-branchial whorls seen in *Brochoadmones milesi* also support this idea, if they are considered modified tooth whorls rather than tooth precursors.

As mentioned in Chapter IV, the internal denticles in thelodonts such as *Loganellia* (Smith and Coates, 2000) are not a good model for the evolutionary origins of teeth. They are not very tooth-like in their growth and patterning. There is also the issue that thelodonts are not usually considered to be the sister group to gnathostomes; instead, the Osteostraci, which lack tooth-like structures as far as known, have that distinction (Donoghue and Sansom, 2002).

There is also the problem of the absence of evidence of true teeth within the placoderms. The only placoderms suspected of having 'teeth' are very derived (Johanson and Smith, 2005), making their 'teeth' unlikely to be homologous to the teeth seen in the Eugnathostomata (Young, 2003). Therefore, it is unlikely that close homologues of eugnathostome teeth existed in either thelodonts or placoderms. From the evidence collected in this study and the similarities among the various dentitions discussed, it seems to me to be likely that the teeth of the Eugnathostomata originated only once in an ancestor not shared with either thelodonts or placoderms.

Future Work

Since a great deal of information about the dentitions of early eugnathostomes has been discovered in this study, new thoughts about the origins and development of teeth arise. Are all tooth whorls homologous to shark tooth families? Are these homologous to the whorls seen in sarcopterygians? What are the relationships between tooth whorls and dentigerous bony plates in acanthodians? How are the various branchial and pharyngeal dentitions related to the bony plates and tooth whorls, if at all? Are they true teeth or denticles? These are just some of the questions posed by the discovery and description of the dentitions from the MOTH locality. Some preliminary answers have been suggested but more work needs to be done before firm conclusions can be drawn.

More histological work should to be done to help clarify these questions. The small-scale CT-scanning done for this study gives some insight into how these different jaws and whorls grew, but more detailed work is required. I believe that thin-sectioning of some of these structures will show small-scale morphological and structural variations within the teeth, as well as indicate how they grew and were added.

For future work, in addition to more histological work, I plan on taking the information obtained in this study and adding the resulting characters to a phylogenetic analysis. I will be basing this on the initial phylogeny by Hanke (2001). I plan on comparing the taxa from MOTH with other well-known acanthodians and putative chondrichthyans from the same time, as well as some primitive sharks (*Doliodus problematicus*, Miller et al., 2003; *Lissodus carlsi*, Botella et al., 2005) and osteichthyan taxa (*Cheirolepis canadensis*, Arratia and Cloutier, 1996). I also plan on adding to the outgroups, including a placoderm (*Bothriolepis*, Janvier, 1996) and an osteostracan (*Ateleaspis tessellate*, Ritchie, 1967). This will hopefully clarify some of the confusion concerning the relationships of these various taxa, and help establish whether the putative chondrichthyans should be definitely assigned to Chondrichthyes.

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